



TAXONOMIC REVIEW OF THE SPECIES GROUPS OF THE GENUS  
*PHYSALAEEMUS* FITZINGER, 1826 WITH REVALIDATION OF THE GENERA  
*ENGYSTOMOPS* JIMÉNEZ-DE-LA-ESPADA, 1872 AND *EUPEMPHIX*  
STEINDACHNER, 1863 (AMPHIBIA, ANURA, LEPTODACTYLIDAE) <sup>1</sup>

(With 6 figures)

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**ABSTRACT:** The species groups of the genus *Physalaemus* are redefined based on morphometrics, external morphology, color patterns, and osteological characters. Seven species groups of *Physalaemus* are recognized: *P. cuvieri* group (eight species), *P. signifer* group (ten species), *P. albifrons* group (four species), *P. deimaticus* group (three species), *P. gracilis* group (five species), *P. henselii* group (three species), and *P. olfersii* group (four species). The genus *Engystomops* Jiménez-de-la-Espada, 1872 is revalidated to include the former *P. pustulosus* group (*sensu* Lynch, 1970). It consists of seven species: *E. petersi* Jiménez-de-la-Espada, 1872 (type-species by monotypy), *E. coloradorum* (Cannatella & Duellman, 1984), *E. guayaco* (Ron, Coloma & Cannatella, 2005), *E. montubio* (Ron, Cannatella & Coloma, 2004), *E. pustulatus* (Shreve, 1941), *E. pustulosus* (Cope, 1864), and *E. randi* (Ron, Cannatella & Coloma, 2004). The genus *Eupemphix* Steindachner, 1863 is revalidated to include *E. nattereri* Steindachner, 1864.

**Key words:** Anura. Leptodactylidae. *Physalaemus*. *Engystomops*. *Eupemphix*.

**RESUMO:** Revisão taxonômica dos grupos de espécies do gênero *Physalaemus* Fitzinger, 1826 com revalidação dos gêneros *Engystomops* Jiménez-de-la-Espada, 1872 e *Eupemphix* Steindachner, 1863 (Amphibia, Anura, Leptodactylidae).

Os grupos de espécies do gênero *Physalaemus* são redefinidos com base em características de morfometria, morfologia externa, padrão de desenho e osteologia. Os sete grupos propostos são: grupo *P. cuvieri* (oito espécies), grupo *P. signifer* (dez espécies), grupo *P. albifrons* (quatro espécies), grupo *P. deimaticus* (três espécies), grupo *P. gracilis* (cinco espécies), grupo *P. henselii* (três espécies) e grupo *P. olfersii* (quatro espécies). O gênero *Engystomops* Jiménez-de-la-Espada, 1872 é revalidado para incluir as espécies previamente pertencentes ao grupo *P. pustulosus* (*sensu* Lynch, 1970), sendo composto por sete espécies: *E. petersi* Jiménez-de-la-Espada, 1872 (espécie-tipo por monotipia), *E. coloradorum* (Cannatella & Duellman, 1984), *E. guayaco* (Ron, Coloma & Cannatella, 2005), *E. montubio* (Ron, Cannatella & Coloma, 2004), *E. pustulatus* (Shreve, 1941), *E. pustulosus* (Cope, 1864) e *E. randi* (Ron, Cannatella & Coloma, 2004). O gênero *Eupemphix* Steindachner, 1863 é revalidado para incluir *E. nattereri* Steindachner, 1863.

**Palavras-chave:** Anura. Leptodactylidae. *Physalaemus*. *Engystomops*. *Eupemphix*.

## INTRODUCTION

The genus *Physalaemus* was erected by FITZINGER (1826) for a single species, *P. cuvieri*, from "America, Brazil" and was only characterized by the presence of slender fingers.

STEINDACHNER (1863) described the genus *Eupemphix* for the species *E. nattereri*, from "Cuyaba

in Mato Grosso, Brasilien". *Engystomops* was erected by JIMENÉZ-DE-LA-ESPADA (1872) for *E. petersi*, from the "Oriente en el Ecuador". LYNCH (1970) combined the species of the genera *Engystomops* Jiménez-de-la-Espada, 1872, *Eupemphix* Steindachner, 1863, and *Physalaemus* Fitzinger, 1826 into a single genus, *Physalaemus*. Currently, the genus *Physalaemus* includes 46 species,

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distributed from southern Mexico to northern Argentina (FROST, 2004; CRUZ & PIMENTA, 2004; RON, COLOMA & CANNATELLA, 2005). LYNCH (1970) recognized four species groups based on the variation of characters analyzed: *P. biligonigerus* group, with greater size than other species of the genus, smooth to loosely-pustular skin, first finger not longer than second, non-elongated inner tarsal tubercle, enlarged, compressed metatarsal tubercle, distinct, disc-like inguinal glands, parotoid glands absent, and premaxillary and maxillary teeth present (except in *P. nattereri*); *P. pustulosus* group, with moderate size, slender to stocky build, tuberculated skin, first finger longer than second, elongated inner tarsal tubercle (except in *P. freibergeri*, and *P. pustulosus*), small, non-compressed metatarsal tubercle, inguinal glands absent, prominent parotoid glands and poorly to well defined flank glands present, premaxillary and maxillary teeth present (except in *P. pustulatus*); *P. signifer* group, with small to moderate size, slender build, smooth skin, first finger shorter than second, no inner tarsal tubercle, non-compressed metatarsal tubercle, small to large inguinal glands, parotoid glands absent, premaxillary and maxillary teeth absent (except in *P. olfersii*); and *P. cuvieri* group, with small to moderate size, slender to stocky build, smooth to warty skin, first finger shorter than second, inner tarsal tubercle present, small, non-compressed metatarsal tubercle (except in *P. albifrons*), small inguinal glands present or absent (except *P. aguirrei* that has large glands), parotoid glands absent, and premaxillary and maxillary teeth present. Additionally, LYNCH (1970) argued that the arrangement of some species in these groups made them relatively heterogeneous.

HEYER (1974, 1975) discussed the phylogenetic relationships among the genus of Leptodactylinae and considered the genus *Physalaemus* monophyletic and as the sister group to *Pleurodema* Tschudi, 1838 or to *Pseudopaludicola* Miranda-Ribeiro, 1926.

CANNATELLA & DUELLMAN (1984) revised the monophyletic *P. pustulosus* group, including four species and defined it by four characters: presence of parotoid glands; elliptical flank glands; warty, pustular skin; and thin dentigerous process of the vomers. CANNATELLA *et al.* (1998) used the characters of advertisement calls, morphology, allozymes, and the 12S and cytochrome oxidase I (COI) mitochondrial to estimate the phylogeny of the species of the *P. pustulosus* group. TÁRANO & RYAN (2002) presented a preliminary phylogenetic analysis of *Physalaemus* and suggested that the

genus consisted of two monophyletic groups, the *P. pustulosus* species group and all others species. Since LYNCH (1970), several species of *Physalaemus* have been described or redescribed and placed in one of those four previously defined groups (BRAUN & BRAUN, 1977; CANNATELLA & DUELLMAN, 1984; CARDOSO & HADDAD, 1985; HEYER & WOLF, 1989; LOBO, 1993; POMBAL & MADUREIRA, 1997; HADDAD & POMBAL, 1998; FEIO, POMBAL & CARAMASCHI, 1999; CARAMASCHI, FEIO & GUIMARÃES NETO, 2003; HADDAD & SAZIMA, 2004; RON, CANNATELLA & COLOMA, 2004; CRUZ & PIMENTA, 2004; RON, COLOMA & CANNATELLA, 2005). Currently, four species are included in the *P. biligonigerus* group; six species in the *P. pustulosus* group; 12 species in the *P. signifer* group; and 19 species in the *P. cuvieri* group. *Physalaemus deimaticus* Sazima & Caramaschi, 1986, *P. rupestris* Caramaschi, Carcerelli & Feio, 1991, and *P. erythros* Caramaschi, Feio & Guimarães-Neto, 2003 are not associated to any species group. However, CARAMASCHI, CARCERELLI & FEIO (1991) and CARAMASCHI, FEIO & GUIMARÃES NETO (2003) suggested that the similarity in morphology and habitat of these three species are an indication that they might constitute a distinct group. Furthermore, several authors noted the need of a revision of the *Physalaemus* species groups (HEYER & WOLF, 1989; LOBO, 1992, 1996; FEIO, POMBAL & CARAMASCHI, 1999; CARAMASCHI, FEIO & GUIMARÃES NETO, 2003).

Herein, based on the analysis of morphometrics, external morphology, color patterns, and osteological characters, we propose a new arrangement of species groups for the genus *Physalaemus* and we revalidate the genus *Engystomops* Jiménez-de-la-Espada, 1872, for the *Physalameus pustulosus* species group (*sensu* LYNCH, 1970), and *Eupemphix* Steindachner, 1863, to accommodate *E. nattereri* Steindachner, 1863.

#### MATERIAL AND METHODS

Specimens examined are deposited in: AL-MN (Adolpho Lutz collection, housed in the Museu Nacional, Rio de Janeiro, Brazil), AMNH (American Museum of Natural History, New York, USA), CFBH (Célio F.B. Haddad collection, deposited in the Departamento de Zoologia, Universidade Estadual Paulista, Rio Claro, Brazil), EI (Eugenio Izecksohn collection, deposited in the Universidade Federal Rural do

Rio de Janeiro, Seropédica, Brazil), FML (Fundación Miguel Lillo, San Miguel de Tucumán, Argentina), MCNAM (Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil), MFL (Museu de Ciência e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil), MNRJ (Museu Nacional, Rio de Janeiro, Brazil), MZUFV (Museu de Zoologia João Moojen de Oliveira, Universidade Federal de Viçosa, Brazil), MZUSP (Museu de Zoologia, Universidade de São Paulo, Brazil), UFRGS (Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil), USNM (National Museum of Natural History, Smithsonian Institution, Washington, USA), and ZUEC (Museu de História Natural, Universidade Estadual de Campinas, Brazil).

Morphometric data were obtained from 972 preserved specimens ( $\sigma = 690$ ;  $\text{♀} = 282$ ) corresponding to 42 species of *Physalaemus*, two species of *Pleurodema* [ $\sigma = 19$ ,  $\text{♀} = 20$ , *P. brachyops* (Cope, 1869) and *P. diplolistris* (Peters, 1870)], and two species of *Pseudopaludicola* [ $\sigma = 21$ ,  $\text{♀} = 8$ , *P. falcipes* (Hensel, 1867) and *P. mineira* Lobo, 1994]. Abbreviations used are as follow: SVL (snout-vent length), HL (head length), HW (head width), ED (eye diameter), IOD (interorbital distance), UEW (upper eyelid width), END (eye-nostril distance), NSD (nostril-snout distance), IND (internarial distance), UL (upper arm length), AL (arm length), HAL (hand length), TL (thigh length), SL (shank length), FL (foot length, from the inner metatarsal tubercle to the distal point of fourth toe). Measurements were taken to the nearest 0.1mm using callipers or an ocular micrometer in a Zeiss stereomicroscope and follow CEI (1980). The Kruskal-Wallis test was performed to verify sexual dimorphism and, if significant, separate analyses were performed for males and females. Principal Component Analysis (PCA) was performed to verify the distribution of the specimens without *a priori* definition of groups in multivariate space. The UPGMA (Unweighted pair-group method using arithmetic averages) was performed to verify the relationship among the species based on the Mahalanobis distances (ZAR, 1999) for fifteen morphometric parameters. Size free discriminant analysis was employed to study the variation between the proposed species groups. The bootstrap method with 1000 pseudoreplications was used to test the robustness of the results

(MAINLY, 2000). All statistic tests were performed with a significance level of 0.05.

The color patterns were determined based only on preserved male specimens.

The external morphological characters were analyzed based on their occurrence, shape, and degree of development and extension, following LYNCH (1971) and CANNATELLA & DUELLMAN (1984); however, some characters and character states were improved and redefined. The patterns proposed by CEI (1980), SAVAGE (1987), HEYER *et al.* (1990), LYNCH & DUELLMAN (1997), and W.R. HEYER (pers. com.) were used to determine the states of the following external characters: glands, texture of skin, snout, canthus rostralis, loreal region, tympanic annulus, folds, tubercles, fingers, fringe on fingers and toes, and vocal sac. Herein, we only described the analysed characters that present significant differences to discriminate genera and species groups.

Cleared and doubled (bone and cartilage) stained skeletal preparations of 27 species of *Physalaemus* were analyzed. The main osteological parameters used were: presence or absence; degree of development; shape; and relationships between bones or part of them. Skeletal preparations follow TAYLOR & VAN DYKE (1985) and osteological nomenclature was based on LYNCH (1971), TRUEB (1973), CANNATELLA & DUELLMAN (1984), DUELLMAN & TRUEB (1986), and TRUEB (1992).

The osteological description of all specimens were performed but only some parameters showed differences enough to characterize the genera and species groups proposed. The following morphometric parameters of osteological characters used were: skull length, measured from the anterior margin of the premaxilla to the posterior margin of the occipital condyle; skull width, measured as the maximum distance between lateral surface of maxillae; the angle between the maxillary ramus and the ventral ramus of the squamosal; length of the cultriform process of the parasphenoid, measured from its anterior tip to the meeting with parasphenoid alae; and parasphenoid alae width, measured between its extremes.

Specimens of two species of *Pleurodema*, *P. brachyops* and *P. diplolistris*, and two species of *Pseudopaludicola*, *P. falcipes* and *P. mineira*, were analyzed for the same external morphological and osteological characters as *Physalaemus* to allow comparisons among genera.

## RESULTS AND DISCUSSION

## CHARACTER ANALYSIS

Morphometry - Sexual dimorphism could be tested for 34 species of the genus *Physalaemus* and, at least, one morphometrical character was significant to indicate dimorphism for 23 species (Tab.1). The main morphometric characters exhibiting dimorphism were HW (for 15 species) and SVL (for 13 species). However, the dimorphic parameters of this study differ from those proposed by LYNCH (1970). Consequently, males and females were analyzed separately in the subsequent statistical tests (HEYER *et al.*, 1994).

Snout-vent length of *Physalaemus* specimens varies from 14 to 50mm for adults (*P. bokermanni* and *P. maximus*, respectively). The species were considered small if the SVL was less than 25mm, of moderate size if the SVL was between 25 and 35mm, and large if the SVL was greater than 35mm. These parameters are similar to those indicated by LYNCH (1970).

The Principal Component Analysis (PCA) was performed with all morphometric characters obtained to determine the degree of discrimination among the specimens examined. All variables were positively correlated with the first principal component, and thus it was interpreted as size. The first principal component represented 94% of the variation in males and 93% in females. This result correlates to the great amount of size variation observed among species of *Physalaemus* and the related taxa examined in these analyses. In order to minimize this effect, a size-free discriminant analysis was performed (SFDA) (REIS, PESSÔA & STRAUSS, 1985).

The UPGMA analysis of males and females, not arranged in *a priori* groups, based on 15 morphometric characters, demonstrated a tendency to form groups (Figs.1-2). The analysis of male characteristics for 42 species of *Physalaemus*, two species of *Pleurodema*, and two species of *Pseudopaludicola*, suggests an arrangement similar to the groups proposed in this study. It resulted in five clusters: (1) species of the *P. gracilis* group; (2) species of the *P. cuvieri* group; (3) species of the *P. signifer* group, (4) species of the *P. deimaticus* group; and (5) species of the *P. albifrons* group. *Physalaemus nattereri* appears closer to *Pleurodema* species than to *Physalaemus*. The analysis of female characteristics including 40 species of *Physalaemus* and all other taxa examined resulted in a less clear arrangement with only four clusters: (1) species of the *P. cuvieri*

group; (2) species of the *P. signifer* group; and (3) species of the *P. gracilis* group, except for *P. erikae*; and (4) species of the *P. olfersii* group. On both analyses, only two species of *P. pustulosus* group demonstrated morphometric affinities (*P. pustulosus* and *P. petersi*).

Table 1- Morphometric parameters with significant values ( $p < 0.05$ ) for sexual dimorphism in examined species of the genus *Physalaemus* (*sensu* LYNCH, 1970).

SPECIES	MORPHOMETRIC PARAMETERS
<i>P. aguirrei</i>	HW, AL, TL, IND, IG
<i>P. albifrons</i>	None significant
<i>P. albonotatus</i>	HW
<i>P. atlanticus</i>	HW, AL, END
<i>P. barrioi</i>	SVL, HW, HL, TL, END, IND
<i>P. biligonigerus</i>	IOD
<i>P. bokermanni</i>	SVL, HW, HL, UL, HAL, TL, FL, ED, UEW
<i>P. caete</i>	Only one female
<i>P. centralis</i>	None significant
<i>P. cicada</i>	None significant
<i>P. coloradorum</i>	SVL, HL, AL, TL, ED, END, IND, NSD
<i>P. crombiei</i>	SVL, HW, HL, AL, TL, END, IOD, IG
<i>P. cuqui</i>	None significant
<i>P. cuvieri</i>	HL, AL, ED
<i>P. deimaticus</i>	No female analysed
<i>P. ephippifer</i>	No female analysed
<i>P. erikae</i>	NSD
<i>P. erytros</i>	Only one female
<i>P. evangelistai</i>	None significant
<i>P. fernandezae</i>	TL
<i>P. fischeri</i>	No female analysed
<i>P. fuscomaculatus</i>	SVL, HW, HL, IG
<i>P. gracilis</i>	UL
<i>P. henselii</i>	SVL, HW, IOD, NSD, IG
<i>P. jordanensis</i>	None significant
<i>P. kroyeri</i>	None significant
<i>P. lisei</i>	SVL, HW, AL, TL
<i>P. maculiventris</i>	SVL, HW, AL, TL, END
<i>P. maximus</i>	Only one female
<i>P. moreirae</i>	None significant
<i>P. nanus</i>	Only one female
<i>P. nattereri</i>	HW, IOD
<i>P. obtectus</i>	SVL, AL, END
<i>P. olfersii</i>	None significant
<i>P. petersi</i>	SVL, HW, HL, AL, TL, ED, IOD, END, IND, NSD
<i>P. pustulatus</i>	No significative
<i>P. pustulosus</i>	SVL, HW
<i>P. riograndensis</i>	None significant
<i>P. rupestris</i>	SVL, TL
<i>P. santafecinus</i>	Only one female
<i>P. signifer</i>	SVL, HW, AL, TL, ED
<i>P. soaresi</i>	Only one female
<i>P. spiniger</i>	HW, HL, ED, IOD

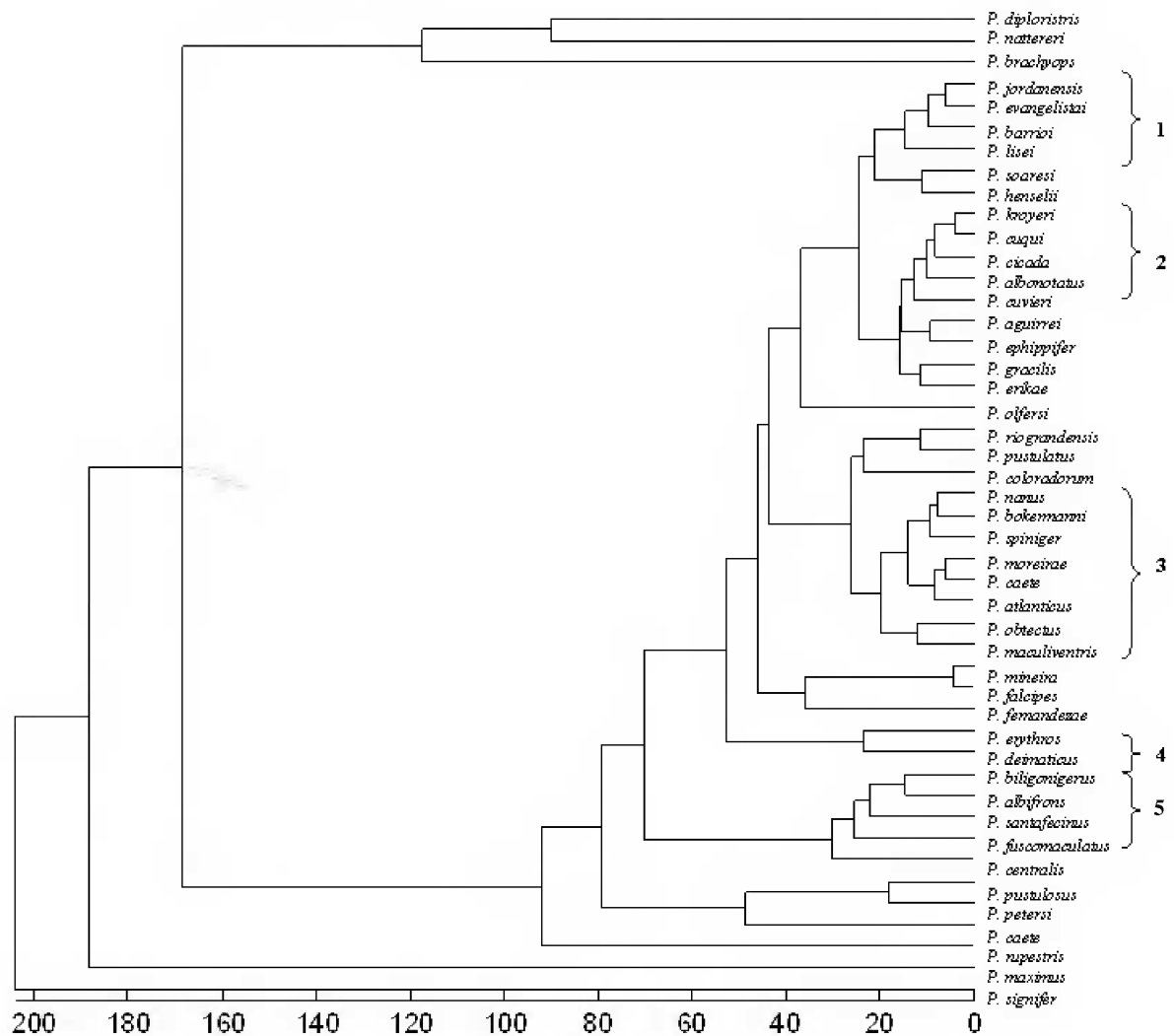


Fig. 1- Grouping analyses (UPGMA) of males of 42 species of *Physalaemus* (*sensu* LYNCH, 1970), two species of *Pleurodema*, and two species of *Pseudopaludicola*, based on 15 morphometric variables, using the similarity matrix obtained from Mahalanobis distances (1-5: clusters).

Size free discriminant analysis of males and females of the proposed groups of *Physalaemus*, *Pleurodema*, and *Pseudopaludicola* were employed (Fig. 3A, B). The canonical plot graphs of male and female data did not show the same discrimination among the groups. The combination of the first two functions corresponded to 72.59% and 66.37% of the entire variation, males and females respectively. Although there is great overlap among some species groups, the males analysis (Fig. 3A) could discriminate some taxa, such as *P. nattereri*, from the other proposed *Physalaemus* species groups.

The variables correlated with the first discriminant function were NS ( $r=0.69$ ,  $p<0.01$ ), HW ( $r= -0.59$ ;  $p<0.01$ ), and AL ( $r= -0.57$ ,  $p<0.01$ ) for males, and NS ( $r=0.62$ ,  $p<0.01$ ), HW ( $r= -0.50$ ,  $p<0.01$ ), and UEW ( $r= -0.42$ ;  $p<0.01$ ) for males. The second

discriminant function showed more correlation with ED ( $r= -0.60$ ,  $p<0.01$ ), HL ( $r= -0.59$ ,  $p<0.01$ ), and SVL ( $r= -0.58$ ,  $p<0.01$ ) for males, and with IOD ( $r=0.53$ ,  $p<0.01$ ), FL ( $r= -0.35$ ,  $p<0.01$ ), and NSD ( $r= -0.33$ ,  $p=0.01$ ) for males.

The analyses of color patterns, external morphology, and osteological characters were performed and the parameters used to define the proposed *Physalaemus* species groups and the genera *Engystomops* and *Eupemphix* are described below:

Color patterns - In dorsal view, eight patterns were identified: (1) many longitudinal dark stripes of variable width (Fig. 4A); (2) two or three inverted V or arrow-shaped blotches, connected or not to each other, darker than background (Fig. 4B); (3) spots of variable number, shape, disposition, and size, associated with tubercles on the skin (Fig. 4C); (4)

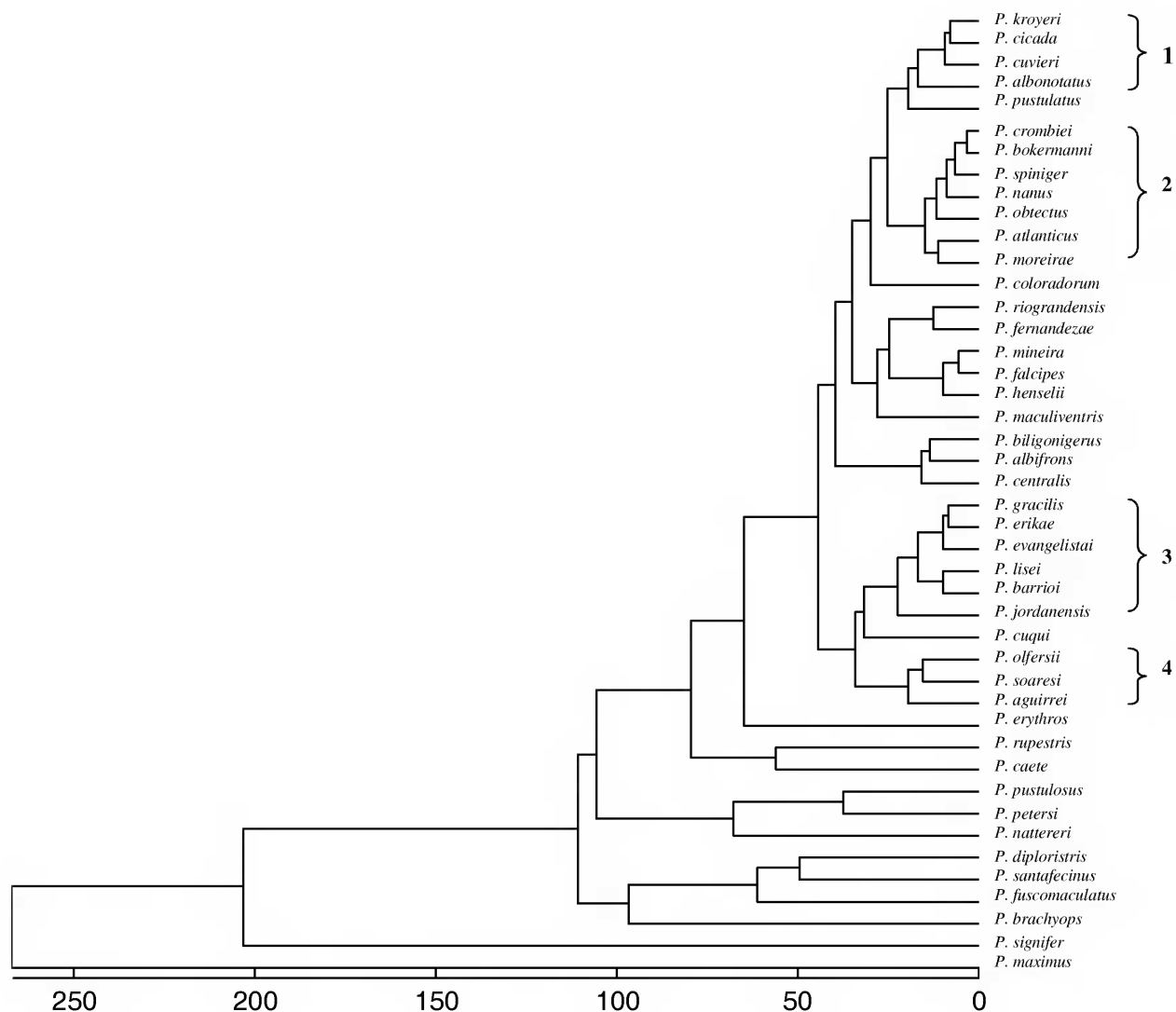


Fig.2- Grouping analyses (UPGMA) of females of 40 species of *Physalaemus* (*sensu* LYNCH, 1970), two species of *Pleurodema*, and two species of *Pseudopaludicola*, based on 15 morphometric variables, using the similarity matrix obtained from Mahalanobis distances (1-4: clusters).

stripes or blotches of irregular shape and width, tending to form an omega-shaped ( $\Omega$ ) mark on the scapular region, with a lighter central area (Fig.4D); (5) many inverted V-shaped stripes, continuous or interrupted (Fig.4E); (6) two longitudinal dark stripes reaching the sacral region, which may be transversally interrupted or/and joined, forming large blotches (Fig.4F); (7) long longitudinal dark stripes, which may be overlapped by more slender and darker stripes, bordering a median light area (Fig.4G); (8) pattern undefined, blotches absent or present, never associated with texture skin (Fig.4H).

In lateral view, seven color patterns were identified: (1) head with alternate dark and light vertical bars, from the tip of the snout to the posterior corner of mouth, a dark stripe extending about 2/3 from

post-orbital area to groin, finishing in a diffuse way (Fig.5A); (2) head with dark and light alternate vertical bars, flanks without a defined pattern (Fig.5B); (3) head light, dark stripe extending from post-orbital region to groin (Fig.5C); (4) head light with a thin dark stripe at the canthus rostralis and a dark stripe extending from post-orbital region to groin (Fig.5D); (5) head dark with light and scattered dots and a dark stripe extending from post-orbital region to groin, edged ventrally by a thin light stripe from post-orbital region to arm insertion (Fig.5E); (6) head and flanks with a dark stripe from snout to groin, edged ventrally by a thin light stripe from snout to arm insertion (Fig.5F); (7) pattern undefined characterized by the absence of dots, blotches, and stripes (Fig.5G).

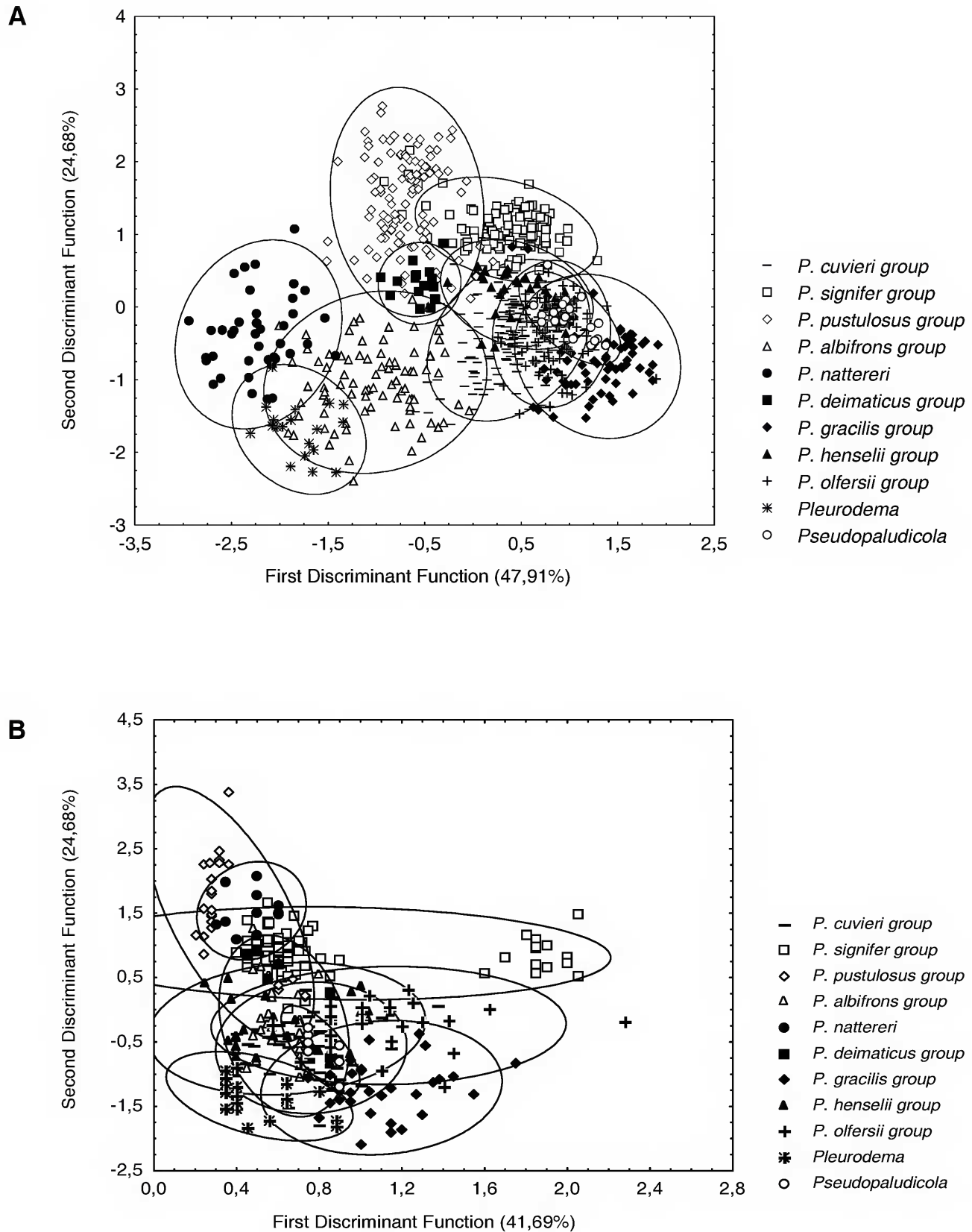


Fig. 3- Canonical analyses of 15 morphometric variables of males (A) and females (B) of *Physalaemus* species groups proposed in the present study, *Physalaemus pustulosus* species group (*sensu* LYNCH, 1970), *P. nattereri*, two species of *Pleurodema*, and two species of *Pseudopaludicola*, with the respective 95% confidence limits ellipse for each group or genera.

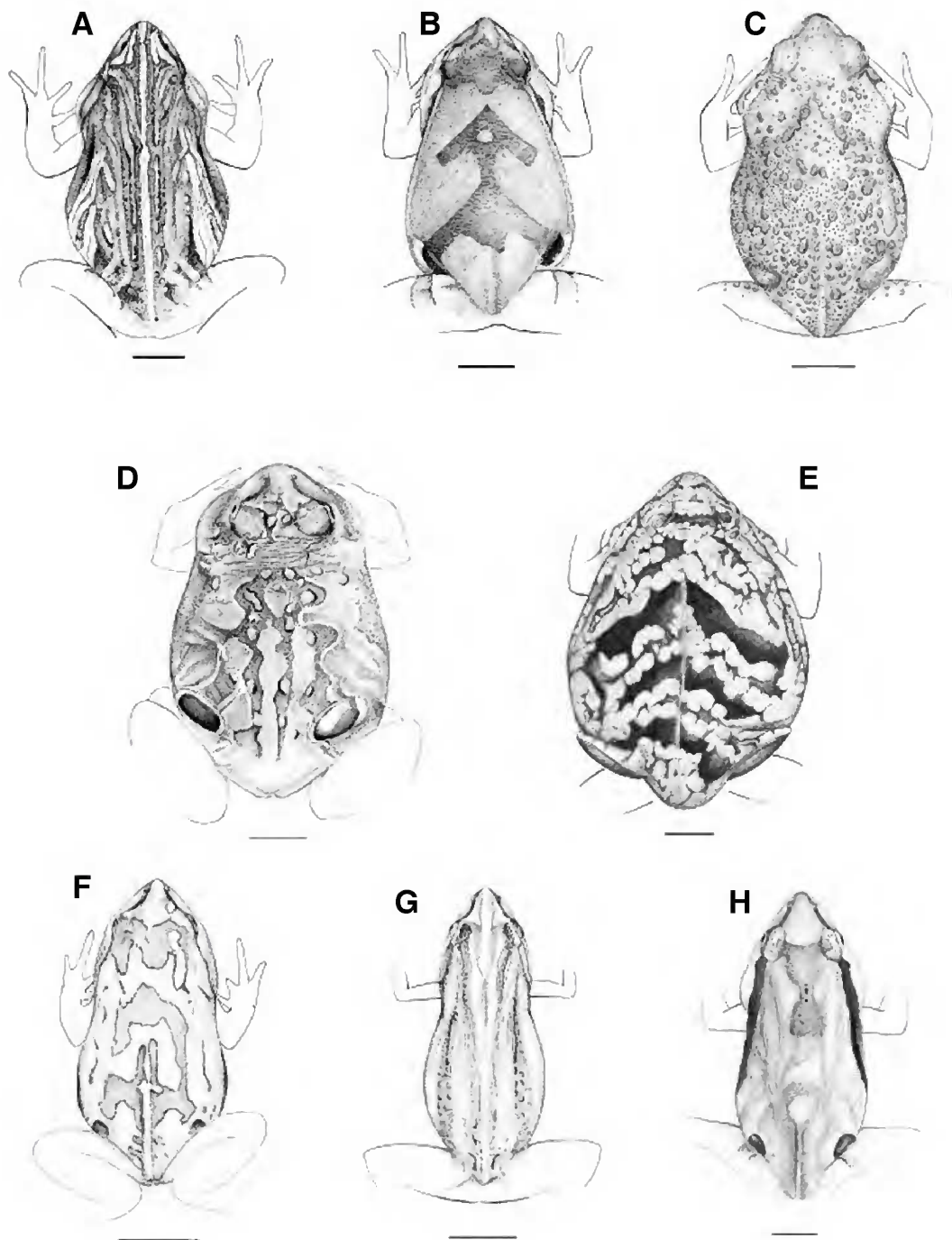


Fig.4- Dorsal color patterns: A) pattern 1 (*P. cuvieri*); B) pattern 2 (*P. signifer*); C) pattern 3 (*E. pustulosus*); D) pattern 4 (*P. biligonigerus*); E) pattern 5 (*E. nattereri*); F) pattern 6 (*P. rupestris*); G) pattern 7 (*P. henselii*); H) pattern 8 (*P. gracilis*). Scale bars = 5mm.

In ventral view, seven patterns were recognized: (1) throat, chest, and belly light, with or without few and small darker dots; (2) throat dark, chest, and belly light, with or without dark blotches; (3) throat and chest dark, belly with dark blotches, more concentrated on anterior region; (4) throat, chest, and belly dark with light, irregular, and

scattered blotches, larger at belly; (5) throat dark, with small light blotches on chest and anterior region of belly, blotches larger on belly, with or without a light median stripe on throat and chest; (6) throat and chest dark, belly light with large, scattered spherical or irregular dark blotches; (7) throat dark, chest and belly marbled.



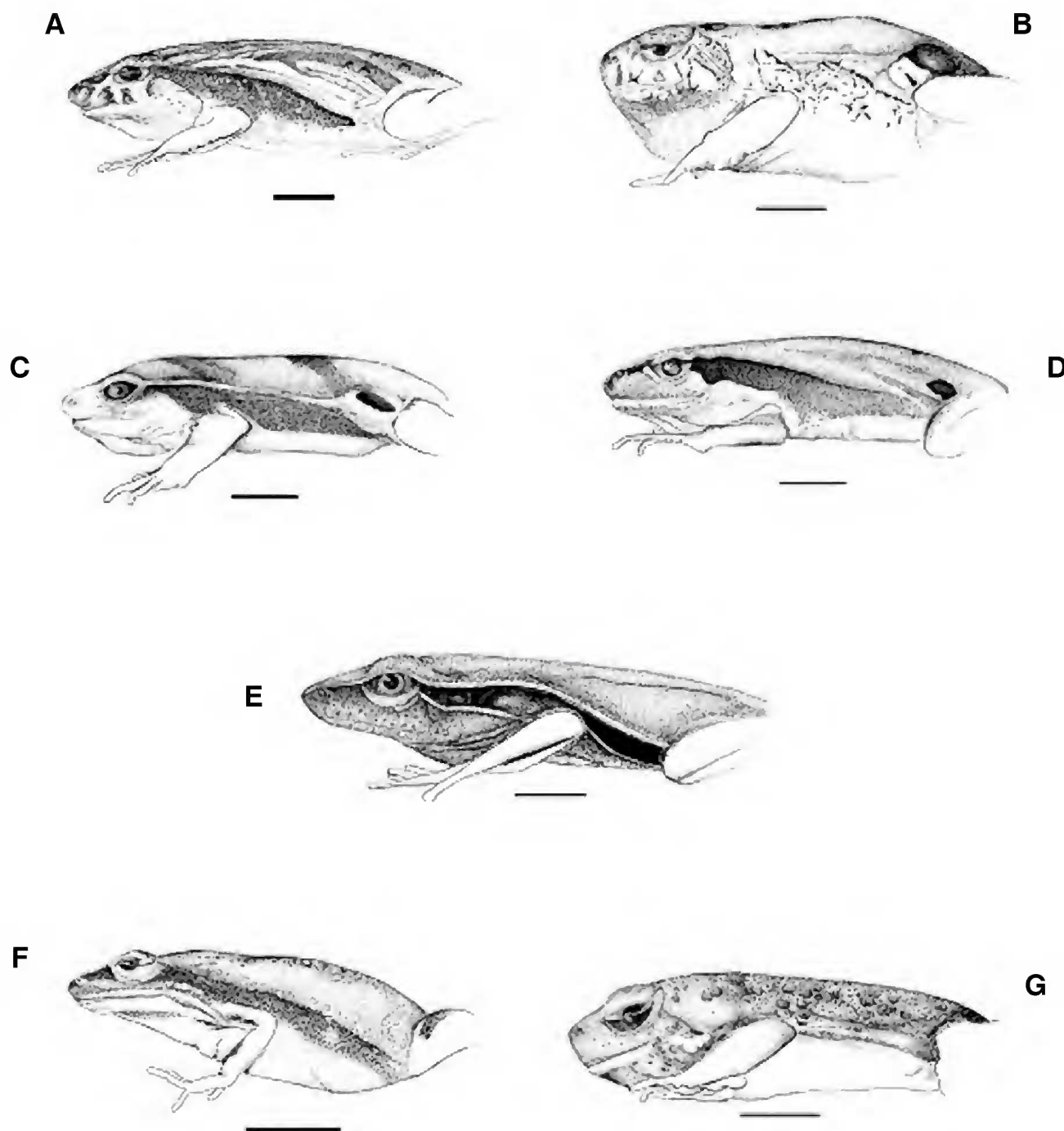


Fig.5- Lateral color patterns: A) pattern 1 (*P. cuvieri*); B) pattern 2 (*P. biligonigerus*); C) pattern 3 (*P. signifer*); D) pattern 4 (*P. gracilis*); E) pattern 5 (*P. olfersii*); F) pattern 6 (*P. henselii*); G) pattern 7 (*E. pustulosus*); Scale bar = 5mm.

**External morphology** - The dorsal skin may be smooth, rugose, and with granules or with tubercles. Additionally, the skin may have long glandular ridges. Flank, inguinal, parotoid, and sacral glands could be present or absent. The ratio between inguinal gland size (measured as their longitudinal length on lateral view) and

snout-vent length is used to characterize them as: small (less than 10%); medium (around 10 to 15%); and large (more than 15%). The inguinal gland may be associated or not with a dark ocellus. The sacral gland is not a useful character because it may be evident or not among specimens of the same species.

Additionally, a thin, longitudinal, and bulky ridge gland located between the eyes and insertion of the arm, and a broad glandular area along the flank, extending from the post-orbital region to the groin, were recorded as present or absent. The latter gland may be continuous or not, but differs from the flank glands by its association with the dorsolateral fold. The snout may be rounded, sub-elliptical, or pointed in dorsal view and rounded, protruding, or acute in lateral view. The canthus rostralis may be rounded or sharp whereas the loreal region is either concave or flat. The tympanic membrane may be evident or not and, if evident may be tuberculated or not. Dorsolateral, supratympanic, and tarsal folds, tarsal and supernumerary tubercles on plantar surfaces were recorded as absent or present (Fig.6A-E). Metatarsal tubercles may be conical or compressed (shovel-like), with distal margins horned or not (Fig.6A-E). The external and internal metatarsal tubercles may have the same length at their bases or not. First and second fingers may have the same length or finger I may be longer or shorter than II. Fringes on the edges of fingers and toes may be present or not, if present, are weakly fringed (Fig.6A-E). A slight webbing between the toes may be present or not (Fig.6A-E). A vocal sac may be well or poorly developed.

Osteological characters – The osteological characters are: (1) ratio between the length and width of skull; (2) the position of the skull-mandible articulation may be anterior to the intersection between the alae and cultriform process of parasphenoid, or at the same transversal plane of the intersection between the alae and cultriform process, or posterior to this intersection; (3) the space between the nasals is narrow or wide; (4) the nasals overlap or not with the anterior margin of the sphenethmoid; (5) the enlargement of the parietal portion of the frontoparietal is present or absent, if absent the bone shape is quite rectangular; (6) the frontoparietals overlap the anterior margin of the exoccipital or not; (7) the frontoparietal fontanelle is exposed or not; (8) the angle between the ventral ramus of the squamosal and maxilla vary from 30° to 70°; (9) the dentigerous process of vomer may be reduced or developed, if developed it may be narrow or broad; (10) the neopalatines are absent or present, if present they are reduced

or developed; (11) the contact between the anterior ramus of pterygoid and the neopalatine is present or absent; (12) the cultriform process of parasphenoid is spike, stick, or subtriangular in shape; (13) the size of cultriform process of the parasphenoid, defined as the ratio between the length of this process to the width of parasphenoid alae, is short (less than to approximately half the width of the parasphenoid alae), medium (greater than half the width of the parasphenoid alae), and long (almost or as long as the width of the parasphenoid alae); (14) the quadratojugal is present or absent; (15) the premaxillary and maxillary teeth are present or absent; (16) the anterior hyale processes is present or absent; (17) the constriction at the base of the alary processes of the hyoid plate is present or absent; (18) the alary processes of the hyoid plate are narrow, slightly broad, or wide.

#### TAXONOMIC DISCUSSION OF THE GENUS *PHYSALAEMUS* FITZINGER, 1826

BOKERMANN (1967) suggested the *Physalaemus gracilis* group for *P. barrioi*, *P. evangelistai*, *P. gracilis*, and *P. jordanensis*, but did not present any characteristics to define it. LYNCH (1970) discussed the heterogeneity of some groups he proposed. He associated *P. albifrons* with the *P. cuvieri* group, but discussed the possibility that this species could be more related to the *P. biligonigerus* group based on the presence of compressed metatarsal tubercles. In addition, he considered the distinctiveness of body glands in *P. olfersii* to place this taxon to its own species group. However, he placed it in the *P. signifer* species group. LOBO (1996) considered *P. albifrons* closer to the *P. biligonigerus* species group. HEYER & WOLF (1989) pointed out the monophyletism of the *P. signifer* species group, except for the inclusion of *P. olfersii*, based on morphological similarity, available habitats, reproductive data, and geographical distribution. FEIO, POMBAL & CARAMASCHI (1999) suggested the *P. olfersii* species group, to accommodate *P. aguirrei*, *P. soaresi*, *P. maximus*, and *P. olfersii*. CARAMASCHI, FEIO & GUIMARÃES-NETO (2003) recognized that, if more morphological characters could be analyzed, *P. deimaticus*, *P. rupestris*, and *P. erythros* could represent a distinct species group.

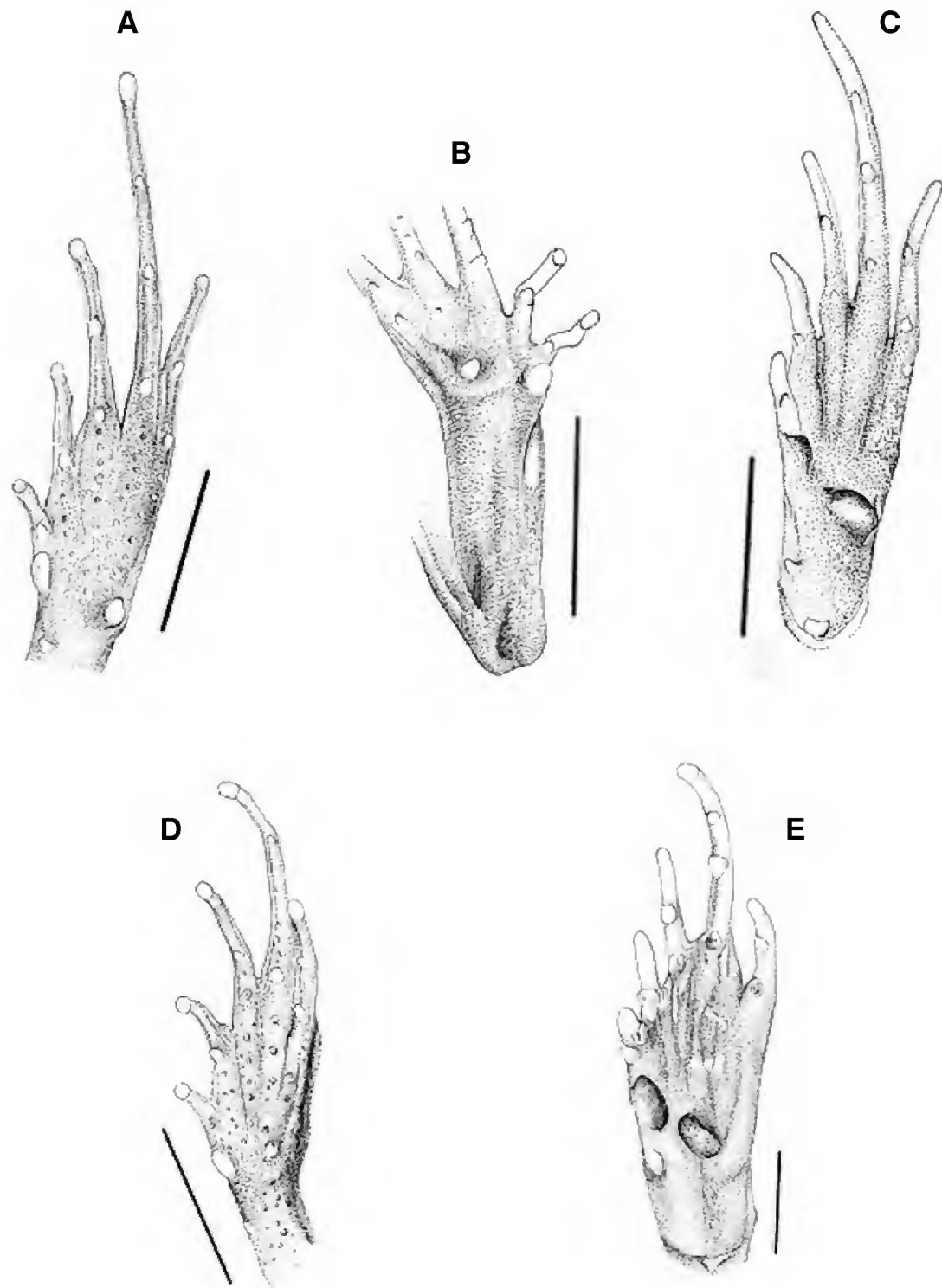


Fig.6- Morphological characteristics on feet: A) presence of tarsal fold, tarsal tubercle, supernumerary tubercles, external and internal metatarsal tubercles conical, without horned distal margins, and fringes on toes (*P. cuvieri*); B) presence of tarsal fold, supernumerary tubercles, and external and internal metatarsal tubercles conical, without horned distal margins, absence of tarsal tubercle (*P. signifer*); C) absence of tarsal fold and supernumerary tubercles, presence of tarsal tubercle, external and internal metatarsal tubercles compressed (shovel-like), with horned distal margins, and fringes on toes (*P. biligonigerus*); D) absence of tarsal fold, presence of tarsal tubercle, supernumerary tubercles, external and internal metatarsal tubercles conical, without horned distal margins, and fringes on toes (*E. pustulosus*); E) absence of tarsal fold, tarsal tubercle, supernumerary tubercles, and fringes on toes, presence of external and internal metatarsal tubercles conical, without horned distal margins, and webbing between toes (*E. nattereri*). Scale bar = 5mm.

*Physalaemus* Fitzinger, 1826*Physalaemus* FITZINGER, 1826.*Paludicola* WAGLER, 1830.*Liuperus* COPE, 1861 "1860".*Gomphobates* REINHARDT & LÜTKEN, 1862 "1861".*Nattereria* STEINDACHNER, 1864.*Iliobates* STEINDACHNER, 1867.Type species – *Physalaemus cuvieri* Fitzinger, 1826.

Diagnosis – The genus *Physalaemus* is composed of leptodactylid anurans characterized by: (1) variable texture of dorsal skin, but never with tubercles; (2) absence of vomerine teeth; (3) absence of hypertrophied antebraquial tubercles; (4) absence of parotoid glands; (5) absence of flank glands; (6) tympanic membrane not evident; (7) skull-mandible articulation never anterior to the transversal plane of the intersection between the alae and cultriform process of parasphenoid; (8) frontoparietals overlapping the anterior margin of exoccipitals; (9) presence of quadratojugals; (10) presence of a developed maxillary process of quadratojugals; and (11) eggs deposited in foam nests.

Geographical distribution – The species of genus *Physalaemus* are distributed from northern to southern South America, east of the Andes.

Through the analysis of morphometrics, color patterns, external morphology, and osteological characters, seven species groups for the genus *Physalaemus* were identified. The groups are:

*Physalaemus cuvieri* Species Group

Contents – *P. albonotatus* (Steindachner, 1864), *P. centralis* Bokermann, 1962, *P. cicada* Bokermann, 1966, *P. cuqui* Lobo, 1993, *P. cuvieri* Fitzinger, 1826, *P. ephippifer* (Steindachner, 1864), *P. erikae* Cruz & Pimenta, 2004, *P. fischeri* (Boulenger, 1890), and *P. kroyeri* (Reinhardt & Lütken, 1862 "1861").

Description – Small to moderate size (21.0-39.6mm); head as long as wide; dorsal color patterns 1, 3, 4, and 8; lateral color patterns 1, 2, and 3; ventral color patterns 1, 2, 3, 4, and 5; variable texture of dorsal skin, but never with tubercles; presence or absence of inguinal glands, if present small and not associated with a dark ocellus; presence or absence of sacral glands is intraspecifically variable; absence of a bulky ridge gland; absence of a broad glandular area along the flanks; snout rounded or sub-elliptical in dorsal view, rounded and protruding in lateral view; canthus rostralis rounded; loreal region concave; presence or absence of dorsolateral fold; presence

or absence of supratympanic fold; presence of tarsal fold, except in *P. fischeri*; presence of tarsal tubercle; presence or absence of supernumerary tubercles; external and internal metatarsal tubercles conical, without horned margins and with the same base length; absence of fringe on fingers and presence or absence on toes; absence of webbing between toes; vocal sac well developed; skull slightly wider than long; skull-mandible articulation at the same transversal plane of intersection between the alae and cultriform process of the parasphenoid; space between nasals narrow, except in *P. cicada*; nasals overlapping the anterior margin of the sphenethmoid; presence of an enlargement of parietal portion of the parietal portion of the frontoparietal; frontoparietal fontanelle not exposed; angle between ventral ramus of squamosal and maxilla vary from 42° to 66°; dentigerous process of vomer developed and broad; presence of developed neopalatines; presence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid spike-shaped, medium sized; presence of premaxillary and maxillary teeth; presence of anterior hyale processes; presence of constriction on the base of alary processes of the hyoid plate; and a slightly broad or broad alary process of the hyoid.

Geographical distribution – Southern to northern South America east of the Andes, from Argentina to Venezuela, in the open formations of Cerrado, Caatinga, Chaco, and Llanos Domains. All species have relatively wide distributions.

*Physalaemus signifer* Species Group

Contents – *P. atlanticus* Haddad & Sazima, 2004, *P. bokermanni* Cardoso & Haddad, 1985, *P. caete* Pombal & Madureira, 1997, *P. crombiei* Heyer & Wolf, 1989, *P. maculiventris* (Lutz, 1925), *P. moreirae* (Miranda-Ribeiro, 1937), *P. nanus* (Boulenger, 1888), *P. obtectus* Bokermann, 1966, *P. signifer* (Girard, 1853), and *P. spiniger* (Miranda-Ribeiro, 1926).

Description – Small to moderate size (14.9-28.5mm); variable relationship between the length and width of head; dorsal color pattern 2; lateral color pattern 3; ventral color patterns 3, 4, 5, and 6; texture of dorsal skin smooth or rugose; presence of small to large inguinal glands, associated with dark ocellus; absence of sacral glands; absence of a bulky ridge gland; absence of a broad glandular area along the flanks; snout rounded or sub-elliptical in dorsal view, protruding in lateral view, except in *P. crombiei*; canthus rostralis rounded or

sharp; loreal region concave; presence of dorsolateral fold, except in *P. crombiei*; presence of supratympanic fold, less evident in some species; presence of tarsal fold; absence of tarsal tubercle; presence or absence of supernumerary tubercles; external and internal metatarsal tubercles conical, without horned margins, and base length of internal longer than external; absence of fringe on fingers and presence or absence on toes; absence of webbing between toes; vocal sac well developed, except in *P. bokermanni*; skull wider than long; skull-mandible articulation posterior to the intersection between the alae and cultriform process of the parasphenoid; space between nasals narrow, except in *P. nanus*; nasals overlapping the anterior margin of sphenethmoid, except in *P. nanus*; presence or absence of an enlargement of parietal portion of frontoparietal; frontoparietal fontanelle not exposed; angle between ventral ramus of squamosal and maxilla vary from 40° to 53°; dentigerous process of vomer developed and thin, except in *P. spiniger*; presence or absence of neopalatines, if present, reduced; absence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid spike-shaped, short or medium sized; presence or absence of premaxillary and maxillary teeth; absence of anterior hyale processes, except in *P. spiniger*; absence of constriction on the base of alary processes; and broad alary processes of hyoid.

Geographical distribution – Atlantic Rain Forest Domain, from the State of Alagoas to Rio Grande do Sul. Some species have wide distribution, as *P. maculiventris* and *P. signifer*; others have restricted occurrence, as *P. bokermanni* and *P. obtectus*.

#### *Physalaemus albifrons* Species Group

Contents – *P. albifrons* (Spix, 1824), *P. biligonigerus* (Cope, 1861), *P. fuscomaculatus* (Steindachner, 1864), and *P. santafecinus* Barrio, 1965.

Description – Small to large size (22.9-47.5mm); head as wide as or wider than long; dorsal color patterns 1 and 4; lateral color patterns 1 and 2; ventral color patterns 1 and 2; texture of dorsal skin smooth, granulated, or with glandular ridges; presence of large inguinal glands, except in some individuals of *P. albifrons*, not associated with a dark ocellus; absence of sacral glands; absence of a bulky ridge gland; absence of a broad glandular area along the flanks; snout rounded in dorsal and lateral views; canthus rostralis rounded; loreal region concave; presence or absence of dorsolateral

fold, if present less evident; presence of supratympanic fold; presence or absence of tarsal fold; presence of tarsal tubercle; presence or absence of supernumerary tubercles; external and internal metatarsal tubercles shovel-like, with horned distal margin and with the same base length; presence or absence of fringe on fingers and toes; presence or absence of webbing between toes; vocal sac well developed; skull wider than long; skull-mandible articulation at the same transversal plane of intersection between the alae and cultriform process of the parasphenoid; space between nasals narrow, except in *P. albifrons*; nasals overlapping the anterior margin of the sphenethmoid; presence of an enlargement of parietal portion of frontoparietal; frontoparietal fontanelle not exposed; angle between ventral ramus of the squamosal and maxilla vary from 46° to 63°; dentigerous process of vomer developed and broad; presence of neopalatines; presence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid spike-shaped, short or medium sized; presence of premaxillary and maxillary teeth; presence of anterior hyale processes; absence of constriction on the base of the alary processes; and broad alary processes of hyoid.

Geographical distribution – South America, from Argentina, Uruguay, and Paraguay to northeastern Brazil, associated with open formations of the Chaco, Cerrado, and Caatinga Domains.

#### *Physalaemus deimaticus* Species Group

Contents – *P. erythros* Caramaschi, Feio & Guimarães-Neto, 2003, *P. deimaticus* Sazima & Caramaschi, 1988, and *P. rupestris* Caramaschi, Carcerelli & Feio, 1991.

Description – Small size (15.9-23.2mm); head wider than long; dorsal color pattern 6; lateral color pattern 3; ventral color pattern 4; texture of dorsal skin rugose; presence of medium to large inguinal glands, associated with dark ocellus; absence of sacral glands; absence of a bulky ridge gland; absence of a broad glandular area along the flanks; snout rounded in dorsal and lateral views; canthus rostralis rounded; loreal region concave; presence or absence of dorsolateral fold; presence or absence of supratympanic fold; presence or absence of tarsal fold; absence of tarsal tubercle; absence of supernumerary tubercles; external and internal metatarsal tubercles conical, without horned distal margin and the base of the internal longer than of

the external; absence of fringe on fingers and presence or absence on toes; absence of webbing between toes; vocal sac poorly developed; skull as long as wide; skull-mandible articulation at the same transversal plane of intersection between the alae and cultriform process of the parasphenoid; space between nasals very narrow; nasals overlapping the anterior margin of the sphenethmoid; presence of an enlargement of parietal portion of frontoparietal; frontoparietal fontanelle not exposed; angle between ventral ramus of squamosal and maxilla about 51°; dentigerous process of vomer reduced; absence of neopalatines; cultriform process of parasphenoid stick-shaped, short; absence of premaxillary and maxillary teeth; presence of anterior hyale processes; absence of constriction on the base of the alary processes; and broad alary processes of the hyoid.

Geographical distribution – Mountains of the State of Minas Gerais, southeastern Brazil. The three species of the group are endemic to their respective type localities (*P. deimaticus* at Serra do Cipó, *P. erythros* at Serra do Itacolomi, and *P. rupestris* at Serra do Ibitipoca).

#### *Physalaemus gracilis* Species Group

Contents – *P. barrioi* Bokermann, 1967, *P. evangelistai* Bokermann, 1967, *P. gracilis* (Boulenger, 1883), *P. jordanensis* Bokermann, 1967, and *P. lisei* Braun & Braun, 1977.

Description – Small to moderate size (18.7-32.5mm); head longer than wide; dorsal color patterns 4 and 8; lateral color pattern 4; ventral color patterns 1, 3, and 5; variable texture of dorsal skin, some with longitudinal glandular ridges; presence of small to medium sized inguinal glands, except in some specimens of *P. lisei*, associated with a dark ocellus; absence of sacral glands; absence of a bulky ridge gland; absence of a broad glandular area along flanks; snout sub-elliptical in dorsal view, protruding in lateral view; canthus rostralis rounded; loreal region concave; presence or absence of dorsolateral fold, if present less evident; presence or absence of supratympanic fold, if present less evident; presence of tarsal fold; presence of tarsal tubercle; presence or absence of supernumerary tubercles; external and internal metatarsal tubercles conical, without horned margins, and base length of the internal longer than of the external; absence of fringe on fingers and presence on toes; absence of webbing between toes; vocal sac well developed; skull slightly longer than wide; skull-mandible articulation posterior to the

intersection between the alae and cultriform process of the parasphenoid; space between nasals wide; nasals overlapping or not the anterior margin of sphenethmoid; presence of an enlargement of parietal portion of frontoparietal; frontoparietal fontanelle not exposed; angle between ventral ramus of the squamosal and the maxilla vary from 33° to 38°; dentigerous process of vomer developed, broad; presence of developed neopalatines; absence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid sticky-shaped, medium sized; presence of premaxillary and maxillary teeth; presence of anterior hyale processes; presence of constriction on the base of the alary processes; and narrow alary processes of the hyoid.

Geographical distribution – Southern to southeastern of Brazil, Uruguay, northern Argentina and Paraguay, occurring at high altitudes (above 600m), except *P. gracilis*.

#### *Physalaemus henselii* Species Group

Contents – *P. fernandezae* (Müller, 1926), *P. henselii* (Peters, 1872), and *P. riograndensis* Milstead, 1960.

Description – Small size (15.3-25.7mm); head longer than wide, except in *P. fernandezae*; dorsal color patterns 4 and 7; lateral color patterns 1 and 6; ventral color patterns 1 and 5; texture of dorsal skin smooth or granulose, with or without long glandular ridges, except in *P. riograndensis*; presence or absence of inguinal glands, if present small to medium sized, not associated with a dark ocellus; absence of sacral glands, except in *P. riograndensis*; presence of a bulky ridge gland; absence of a broad glandular area along the flanks; snout rounded or sub-elliptical in dorsal view, rounded or protruding in lateral view; canthus rostralis rounded; loreal region concave; absence of dorsolateral fold; presence of supratympanic fold; presence of tarsal fold; presence or absence of tarsal tubercle; presence of supernumerary tubercles; external and internal metatarsal tubercles conical, without horned margins, and the base length of the internal longer than of the external, except in *P. fernandezae*; absence of fringe on fingers and presence or absence on toes; absence of webbing between toes; vocal sac well developed; variable relation between length and width of skull; skull-mandible articulation posterior to the intersection between the alae and cultriform process of the parasphenoid; space between nasals narrow; nasals not overlapping the anterior margin of the

sphenethmoid; presence of an enlargement of parietal portion of frontoparietal; frontoparietal fontanelle exposed, except in *P. riograndensis*; angle between ventral ramus of the squamosal and the maxilla vary from 34° to 45°; dentigerous process of vomer developed, thin; presence of developed or reduced neopalatines; presence or absence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid subtriangular-shaped, medium or long sized; presence of premaxillary and maxillary teeth; presence of anterior hyale processes; presence of constriction on the base of alary process; and narrow alary processes of the hyoid.

Geographical distribution – Southern Brazil, Uruguay, and Argentina, occurring in open areas.

#### *Physalaemus olfersii* Species Group

Contents – *P. aguirrei* Bokermann, 1966, *P. maximus* Feio, Pombal & Caramaschi, 1999, *P. olfersii* (Lichtenstein & Martens, 1856), and *P. soaresi* Izecksohn, 1965.

Description – Small to large size (20.0-48.9mm); head as long as or longer than wide; dorsal color patterns 4 and 8; lateral color pattern 5; ventral color pattern 5; texture of dorsal skin smooth or rugose; presence or absence of inguinal glands, if present small to medium size, and not associated with a dark ocellus; absence of sacral glands; absence of a bulky ridge gland; presence of a broad glandular area along the flanks; snout sub-elliptical or pointed in dorsal view, protruding or acute in lateral view; canthus rostralis sharp; loreal region flat; presence of dorsolateral fold; presence or absence of supratympanic fold; presence of tarsal fold; presence or absence of tarsal tubercle; presence or absence of supernumerary tubercles; external and internal metatarsal tubercles conical, without horned distal margin and the base length of the internal longer than of the external; absence of fringe on fingers and presence on toes; absence of webbing on toes; vocal sac developed; skull wider than long, except in *P. soaresi*; skull-mandible articulation posterior to the intersection between the alae and cultriform process of the parasphenoid; space between nasals narrow, except in *P. soaresi*; nasals overlapping the anterior margin of sphenethmoid, except in *P. soaresi*; presence or absence of an enlargement of parietal portion of frontoparietal; frontoparietal fontanelle not exposed; angle between ventral ramus of squamosal and maxilla 40° to 52°; dentigerous process of

vomer developed, thin or broad; neopalatines developed; absence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid spike-shaped, medium sized; presence of premaxillary and maxillary teeth; presence of anterior hyale process; presence of constriction on the base of alary process; and broad alary processes of the hyoid.

Geographical distribution – Atlantic Rain Forest Domain, from the State of Bahia to Santa Catarina, Brazil.

#### TAXONOMIC DISCUSSION OF THE GENUS *ENGYSTOMOPS* JIMÉNEZ-DE-LA-ESPADA, 1872

CANNATELLA & DUELLMAN (1984) considered the *P. pustulosus* species group (*sensu* LYNCH, 1971) as monophyletic based on four characteristics: (1) presence of flank glands; (2) presence of parotoid glands; (3) warty, pustular skin; and (4) dentigerous process of the vomer thin and spikelike. Within this species group, two clades were identified, one found northwest of the Andes (*P. coloradorum* and *P. pustulatus*), the other in northeast of the Andes (*P. petersi* and *P. pustulosus*). Characters derived from advertisement calls, morphology, allozymes, and the sequences of the mitochondrial ribosomal gene (12S) and the cytochrome oxidase I mitochondrial gene were used to estimate the phylogeny of frogs of the *P. pustulosus* group by CANNATELLA *et al.* (1998). In all trees, except that based on calls, these authors considered the *P. pustulosus* species group as monophyletic. TÁRANO & RYAN (2002) presented a phylogeny supporting a monophyletic *P. pustulosus* species group and separating it from all other analyzed species of the genus *Physalaemus*. RON, CANNATELLA & COLOMA (2004) described two new species (*P. randi* and *P. montubio*) and associated them to the *P. pustulosus* species group. These authors included both species in the northwestern South American clade, with *P. coloradorum* and *P. pustulatus*, by the absence of tarsal tubercles and narrow stalk of the alary process of the hyoid (*P. petersi* and *P. pustulosus* present tarsal tubercles and a broad alary process of the hyoid). RON, COLOMA & CANNATELLA, 2005 described *P. guayaco* as a species of the *P. pustulosus* group and associated it to the clade distributed west of the Andes, sister to *P. petersi* and *P. pustulosus*. Morphometric and morphological characteristics analyzed for *P. coloradorum*, *P. petersi*, *P. pustulatus*, and *P. pustulosus*, as well as osteological characteristics for *P. petersi* and *P. pustulosus*,

obtained in the present study and from literature reports (CANNATELLA & DUELLMANN, 1984; CANNATELLA *et al.*, 1998; TÁRANO & RYAN, 2002; RON, CANNATELLA & COLOMA, 2004; and RON, COLOMA & CANNATELLA, 2005) allow us to place the six recognized species of the *P. pustulosus* species group in the genus *Engystomops* Jiménez-de-la-Espada, 1872.

CANNATELLA & DUELLMANN (1984), CANNATELLA *et al.* (1998), TÁRANO & RYAN (2002), RON, CANNATELLA & COLOMA (2004), and RON, COLOMA & CANNATELLA (2005) pointed the presence of a thin dentigerous process of the vomer as a synapomorphy for the *P. pustulosus* species group. However, in our analysis this characteristic was present on some species of *P. signifer* group and the studied specimen of *P. pustulosus* has a broad dentigerous process of vomer. Furthermore, the character "finger I longer than finger II", noted by CANNATELLA & DUELLMANN (1984) as synapomorphy for the northeastern South American clade (*P. petersi* and *P. pustulosus*) resulted as polymorphic in our analyses. In *P. petersi*, finger I is longer than finger II. However, in 57 specimens of *P. pustulosus*, the observed variation of length of finger I and II was: 34 (59,65%) presented finger II longer than finger I; 19 (33,33%) had both fingers with the same size; and in four specimens (7,02%) had finger I longer than finger II. Herein, 19 studied specimens of *P. pustulosus* were also included in CANNATELLA & DUELLMANN (1984) analysis.

*Engystomops* Jiménez-de-la-Espada, 1872  
revalidated

*Engystomops* JIMÉNEZ-DE-LA-ESPADA, 1872.

*Peralaimos* JIMÉNEZ-DE-LA-ESPADA, 1875.

*Mycrophryne* COPE, 1876 "1875".

*Paludicola* BOULENGER, 1882 (part).

*Physalaemus* - PARKER, 1927 (part).

*Physalaemus* - LYNCH, 1970 (part).

Type species – *Engystomops petersi* Jiménez-de-la-Espada, 1872.

Contents – *E. coloradorum* (Cannatella & Duellman, 1984), *E. guayaco* (Ron, Coloma & Cannatella, 2005), *E. montubio* (Ron, Cannatella & Coloma, 2004); *E. petersi* Jiménez-de-la-Espada, 1872, *E. pustulatus* (Shreve, 1941), *E. pustulosus* (Cope, 1864), and *E. randi* (Ron, Cannatella & Coloma, 2004).

Original description of *Engystomops* – "Cuerpo obeso, extremidades esbeltas; cabeza corta, deprimida y lisa; boca pequeña; ojos regulares;

tímpano visible; parótidas muy pequeñas; lengua estrecha, prolongada y algo elíptica; dedos libres y con las protuberancias infra-articulares muy marcadas, así como las de las palmas y plantas; piel glandulosa. Esternon móvil ó bufoniforme con precoracóides y coracóides, muy poco arcífero; manubrio rudimentario, casi nulo; jifisterno bien desarrollado; vértebra sacra con as diapófisis moderadamente dilatadas, y con su cuerpo soldado con la última lumbar; falanges terminales en forma de áncora ó hierro de anijada.

Este género pudiera describirse en dos palabras: *Engystoma* con parótidas."

Diagnosis – The genus *Engystomops* is characterized by: (1) texture of dorsal skin tuberculated; (2) absence of vomerine teeth; (3) absence of hypertrophied antebrachial tubercles; (4) presence of parotoid glands; (5) presence of flank glands; (6) tympanic membrane evident; (7) skull-mandible articulation anterior to the transversal plane of the intersection between the alae and cultriform process of the parasphenoid; (8) frontoparietals overlapping the anterior margin of exoccipitals; (9) quadratojugals present; (10) maxillary process of quadratojugals present and developed; and (11) eggs deposited in foam nests.

Description – Small to large size (14.9-38.6mm); variable relation between head length and width; dorsal color patterns 1, 3 and 4, generally associated with granulated pattern; lateral color patterns 1, 2 and 7; ventral color patterns 1, 2, 3, 4, 5, and 6; texture of dorsal skin with tubercles; absence of inguinal glands; absence of sacral glands; absence of a bulky ridge gland; absence of a broad glandular area along the flanks; snout rounded, sub-elliptical, or pointed in dorsal view, rounded or protruding in lateral view; canthus rostralis rounded; loreal region flat to convex; tympanic membrane exposed, tuberculated or not; absence of a dorsolateral fold; presence or absence of supratympanic fold, if present short; presence of tarsal fold; presence or absence of tarsal tubercle; presence of supernumerary tubercles; external and internal metatarsal tubercles conical, without horned distal margin and the base length of the internal longer than of the external; absence of fringe on fingers and presence or absence on toes; vocal sac developed; space between nasals narrow; nasals overlapping the anterior margin of sphenethmoid; presence of a slight enlargement of parietal portion of the frontoparietal; frontoparietal fontanelle not exposed; angle between the ventral ramus of the squamosal and the maxilla about 50°;



dentigerous process of vomer developed, thin; neopalatines developed; presence or absence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid subtriangular-shaped, medium sized; presence or absence of premaxillary and maxillary teeth; presence of anterior hyale processes; presence or absence of constriction on the base of the alary processes; and broad or narrow alary processes of the hyoid.

Geographical distribution – Southern Mexico to northern South America. *Engystomops petersi* and *E. pustulosus* occurs eastern of the Andes and *E. coloradum*, *E. montubio*, *E. pustulatus*, *E. randi*, and *E. guayaco* are western species.

Remarks – In the original description of the genus *Engystomops*, a fusion between the sacral and the last lumbar vertebra was indicated (JIMÉNEZ-DE-ESPADA, 1872). The two cleared-and-stained specimens examined for this study exhibited no such fusion, suggesting that it could be variation in the degree of ossification among specimens. CANNATELLA & DUELLMAN (1984) described some osteological characteristics of the *P. pustulosus* species group (*sensu* LYNCH, 1970), using a large number of specimens, but did not reported any case of fused vertebrae.

#### TAXONOMIC DISCUSSION OF THE GENUS *EUPEMPHIX* STEINDACHNER, 1863

LYNCH (1970) argued that the genus *Eupemphix* Steindachner, 1863 and *Physalaemus* Fitzinger, 1826 were classically separated based on the presence or absence of maxillary teeth. This author added that inner tarsal tubercle was a second characteristic used to partition the paludicoline genera and that the genera have entirely discordant variation of both of these features. So, these two genera were combined under *Physalaemus*. LYNCH (1970) included the unique species of *Eupemphix*, as *Physalaemus nattereri*, in the *P. biligonigerus* species group and pointed the absence of an inner tarsal tubercle for this species, discording to the literature. The specimens of *P. nattereri* studied in the present work did not have any tarsal tubercles. Some specimens presented a reduced tarsal fold and its proximal portion could be slightly elevated, what could be confused, at a glance, with a tubercle. Comparisons of this species with others of the genera *Physalaemus* and *Engystomops* indicate that the revalidation of *Eupemphix* Steindachner, 1863 is appropriate.

*Eupemphix* Steindachner, 1863, revalidated

*Eupemphix* STEINDACHNER, 1863.

*Paludicola* - BOULENGER, 1882 (part), BOETTGER, 1885 (part).

*Physalaemus* - PARKER, 1927 (part), LYNCH, 1970 (part).

Type species – *Eupemphix nattereri* Steindachner, 1863.

Contents – *E. nattereri* Steindachner, 1863.

Original description of *Eupemphix* – “Habitus corporis, glandulae lombares, processus transversus vertebrae ut in genere *Pleurodema*; dentes maxillaries et palatini nulli; lingua oblonga, angustissima parva, parte posteriore libera, integra; tympanum latens vel distinctum; digiti antici fissi, postici semipalmati; planta tuberculis duobus valde prominentibus; saccus gularis internus in maribus.”

Diagnosis – The genus *Eupemphix* is characterized by: (1) texture of dorsal skin smooth; (2) absence of vomerine teeth; (3) absence of hypertrophied antibrachial tubercles; (4) absence of parotoid glands; (5) absence of flank glands; (6) tympanic membrane not evident; (7) skull-mandible articulation at anterior to the intersection between the alae and cultriform process of parasphenoid; (8) frontoparietals not overlapping the anterior margins of exoccipitals; (9) presence of quadratojugals; (10) maxillary process of quadratojugals present, developed; and (11) eggs deposited in foam nests.

Description – Stocky body, moderate to large size (29.8-50.6mm); head wider or as wide as long; interorbital distance and eye diameter of the same size; dorsal color pattern 5; lateral color pattern 2; ventral color pattern 7; dorsal skin smooth; presence of large inguinal glands with dark ocellus; absence of sacral glands; absence of a bulky ridge gland; absence of a broad glandular area along the flanks; snout rounded in dorsal and lateral views, canthus rostralis rounded; loreal region concave; absence of dorsolateral fold; presence or absence of supratympanic fold; presence or absence of tarsal fold, if present reduced; absence of tarsal tubercle; absence of supernumerary tubercles on feet; external and internal metatarsal tubercles shovel-like, with horned distal margin and the base length of the internal longer than the external; absence of fringe on fingers and presence on toes; presence of webbing between toes; vocal sac well developed; rounded inner edge of nasals, making them slightly separated; nasals overlapping the anterior margin

of sphenethmoid; presence of an enlargement of parietal portion of frontoparietal; frontoparietal fontanelle not exposed; angle between the ventral ramus of the squamosal and the maxilla about 50°; dentigerous process of vomer developed, broad; presence of developed neopalatines; presence of contact of anterior ramus of pterygoid and neopalatine; cultriform process of parasphenoid spike-shaped, short sized; absence of premaxillary and maxillary teeth; absence of anterior hyale processes; absence of constriction on the base of alary process of the hyoid plate; and broad alary processes of the hyoid.

Geographical distribution – Open areas of central and southeastern Brazil, Argentina, Paraguay, and Bolivia.

#### TAXONOMIC COMPARISONS AMONG RELATED GENERA

The genus *Physalaemus* differs from *Pleurodema* by the presence of quadratojugals and absence of vomerine teeth (absence of quadratojugals and presence of vomerine teeth in *Pleurodema*); from *Pseudopaludicola* by the presence of developed maxillary processes of quadratojugals, eggs deposited in foam nests, and by the absence of hypertrophied antibrachial tubercles (absence of maxillary processes of quadratojugals, eggs not deposited in foam nests, and presence of hypertrophied antibrachial tubercles in *Pseudopaludicola*). The genus *Physalaemus* differs from *Engystomops* by having a smooth to granulated dorsum texture and absence of parotoid and flank glands (tuberculated dorsum texture, presence of parotoid and flank glands in *Engystomops*). The genus *Physalaemus* differs from *Eupemphix* by the skull-mandible articulation never anterior to the intersection between the alae and cultriform process of parasphenoid and frontoparietals overlapping the anterior margins of exoccipitals (skull-mandible articulation anterior to the transversal plane of the intersection between the alae and cultriform process of parasphenoid and frontoparietals not overlapping the anterior margins of exoccipitals in *Eupemphix*).

The genus *Engystomops* differs from *Pleurodema* by the presence of quadratojugals and absence of vomerine teeth (absence of quadratojugals and presence of vomerine teeth in *Pleurodema*); from *Pseudopaludicola* by the presence of developed maxillary processes of quadratojugals, eggs deposited in foam nests, and by the absence of hypertrophied antibrachial tubercles (absence of maxillary

processes of quadratojugals, eggs not deposited in foam nests, and presence of hypertrophied antibrachial tubercles in *Pseudopaludicola*). The genus *Engystomops* differs from *Eupemphix* by presence of parotoid and inguinal glands, dorsal skin tuberculated, external and internal metatarsal tubercles conical, without horned distal margins, presence of supernumerary tubercles on feet, frontoparietals overlapping the anterior margins of exoccipitals (absence of parotoid and inguinal glands, dorsal skin smooth, external and internal metatarsal tubercles shovel-like, with horned distal margin, absence of supernumerary tubercles on feet, and frontoparietals not overlapping the anterior margin of exoccipitals in *Eupemphix*). The genus *Eupemphix* differs from *Pleurodema* by presence of quadratojugals and absence of vomerine teeth (absence of quadratojugals and presence of vomerine teeth in *Pleurodema*); from *Pseudopaludicola*, by the presence of developed maxillary processes of quadratojugals, eggs deposited in foam nests, and by the absence of hypertrophied antibrachial tubercles (absence of maxillary processes of quadratojugals, eggs not deposited in foam nests, and presence of hypertrophied antibrachial tubercles in *Pseudopaludicola*).

#### SPECIMENS EXAMINED

##### Alcohol Preserved Specimens

*Physalaemus aguirrei* – BRAZIL: BAHIA: Caravelas: MNRJ 28442; Mucuri: MNRJ 19276-19277, MNRJ 19279; Nova Viçosa: MNRJ 19039-19045. ESPÍRITO SANTO: Reserva Sooretama, Linhares: MNRJ 4024 (paratype), EI 5746 (paratype), MNRJ 22753-22800; Conceição da Barra: MNRJ 20938-20943. MINAS GERAIS: Nanuque: MCNAM 2915, MCNAM 3027-3030, MCNAM 3032-3034, MCNAM 3316-3324.

*Physalaemus albifrons* – BRAZIL: MARANHÃO: Barreirinha: MNRJ 24216-24226. CEARÁ: Brejo Santo: MNRJ 14940-14942, MNRJ 24059, MNRJ 24062-24072; Mucuripe, Fortaleza: MNRJ 6636-6674; Fortaleza: MNRJ 1125, MNRJ 6636-6676. SERGIPE: Santa Luzia do Itanhý: MNRJ 17976-17981. BAHIA: Barreiras: MNRJ 1094-1096; Bom Jesus da Lapa: MNRJ 114-116, MNRJ 1094-1096, MNRJ 1113, MNRJ 1102-1104, MNRJ 1089-1091; Juazeiro: MNRJ 1105; MZUSP 76521, MZUSP 82303. MINAS GERAIS: Lageado: MNRJ 27180-27189; Manga: MNRJ 27179, MNRJ 21743-21745; Porteirinha: MCNAM 206-209, MCNAM 213-216.

*Physalaemus albonotatus* – BOLÍVIA: SANTA CRUZ: San Antonio de Parepiti: AMNH 144358-144361. ARGENTINA: CORRIENTES: Loreto, San Miguel: UFRGS 1938-1942. BRAZIL: MATO GROSSO: Miranda: MNRJ 12734-12764; Rosário do Oeste: AMNH 72043, USNM 165179, EI 2767-2768; Barra do Tapirapé: AMNH 92634-92640.

*Physalaemus atlanticus* – BRAZIL: SÃO PAULO: Picinguaba, Ubatuba: MNRJ 35115-35118 (paratypes).

*Physalaemus barrioi* – BRAZIL: SÃO PAULO: Campo de Fruticultura da Serra da Bocaina, São José do Barreiro: MZUSP 82358 (holotype), MZUSP 84821-84835, MZUSP 84839, MZUSP 84842, AMNH 79862, CFBH 227, ZUEC 6472; Arapeí: ZUEC 6985-6986, ZUEC 6993.

*Physalaemus biligonigerus* – BOLÍVIA: SANTA CRUZ: AMNH 144362-144370, AMNH 144371-144385, AMNH 144432-144433. BRAZIL: SANTA CATARINA: MNRJ 31128-31153. RIO GRANDE DO SUL: General Câmara: UFGRS 1924-1929; Uruguaiana: UFGRS 1776; Tramandaí: UFGRS 1619; Parque Estadual de Itapoã, Viamão: UFGRS 1319-20, UFGRS 1342. PARAGUAI: Chaco Paraguuaio: AMNH 23807; Colônia Nueva, Itália Villeta: AMNH 50669-50671. URUGUAI: RIO NEGRO: MNRJ 28554.

*Physalaemus bokermanni* – BRAZIL: SÃO PAULO: Santo André: MZUSP 59551 (holotype), MZUSP 59552 (paratype), ZUEC 6845; São Bernardo do Campo: MZUSP 125992-126002.

*Physalaemus caete* – BRAZIL: ALAGOAS: Passo do Camaragibe: MNRJ 9712-9717, Murici MNRJ 9803 (holotype), MNRJ 9801-9802 (paratopotypes), MNRJ 9804-9805 (paratopotypes), MNRJ 9848-9850 (paratopotypes).

*Physalaemus centralis* – BRAZIL: GOIÁS: Silvânia: MNRJ 17425. MATO GROSSO: Rio Coluene, Xingu: MZUSP 73720 (alotype), AMNH 68371-68372 (paratypes), AMNH 73730, EI 2923 (ex-WCAB 8124), MNRJ 14220-14221 (paratypes). MINAS GERAIS: Belo Horizonte: CFBH 1479-1480; Buritis: MCNAM 3274; Conselheiro Mata, Diamantina: MCNAM 592; Lagoa Santa: MCNAM 1702, MCNAM 1816; Manga: MNRJ 26844; Pirapora e Buritizeiro: MNRJ 26510-26513; Pirapora: MNRJ 25487-25501; Porteirinha: MCNAM 217; Riacho dos Machados: MCNAM 292; UHE Igarapava, Sacramento e Conquista: MNRJ 26845-26847; Santana do Riacho: MCNAM 2702-2714, MCNAM 2737, MCNAM 3145-3146; Vale do Peruaçu, Vargem Grande: MCNAM 1030-1031;

Várzea da Palma: MNRJ 27176-27178; Várzea da Palma e Pirapora: MNRJ 26505-26509. SÃO PAULO: Corumbataí: CFBH 1340, CFBH 2057; Botucatu: EI 7845-7847; Emas: MZUSP 96095-96096 (paratypes).

*Physalaemus cicada* – BRAZIL: CEARÁ: Brejo Santo: MNRJ 24060, MNRJ 28552-28553. BAHIA: Maracás: MZUSP 73720 (WCAB 32087, alotype), EI 6152 (WCAB 32088, paratype), AMNH 78232 (paratype), MZUSP 96095 (WCAB 6532, paratype), MZUSP 96095 (WCAB 6532, paratype); Joazeiro: ZUEC 7878-7888; Curaçá: ZUEC 7900-7905; MZUSP 83562-83563, MZUSP 83570; MZUSP 83573-83575; Carnaíba: MZUSP 83577. MINAS GERAIS: Matias Cardoso: MNRJ 21750-21752; Pedra Azul: MZUSP 88844, MZUSP 88847, MZUSP 88849-88850, MZUSP 88858; MZUSP 88860, MZUSP 88874.

*Physalaemus crombiei* – BRAZIL: BAHIA: Nova Viçosa: MNRJ 18923. ESPÍRITO SANTO: Aracruz: MNRJ 17222-17245, MNRJ 17694-17704; Reserva Nova Lombardia, Santa Teresa: MZUSP 66253-66281 (paratypes); Santa Teresa: MNRJ 28300-28304, MNRJ 30875.

*Physalaemus cuqui* – ARGENTINA: SALTA: Departamento Orán, Intendencia de la Finca El Arrazayál: FML 04476-1, FML 04476-3; Departamento Ledesma, Parque Nacional Calilegua: FML 05082-5, FML 05082-6, FML 05082-8; Departamento Anta, Finca Pozo Largo: FML 05379; Departamento Anta, Finca San Javier: FML 05644-1, FML 05644-4, FML 05644-5, FML 05644-7; Departamento Ledesma, Yuto: FML 01281-2.

*Physalaemus cuvieri* – BRAZIL: MARANHÃO: São Pedro das Águas Brancas: MNRJ 24255-24266. BAHIA: Caetitê: MNRJ 25033-25040. DISTRITO FEDERAL: Brasília: MCNAM 2796-2809. GOIÁS: Luziânia: MCNAM 3007-3014; São João da Aliança: MNRJ 27762-27763; UHE Serra da Mesa, Minaçu: MNRJ 20268-20282; Chapada dos Veadeiros: MNRJ 478, MNRJ 5502-5521. ESPÍRITO SANTO: Santa Teresa: MNRJ 28378. MINAS GERAIS: Catas Altas: MCNAM 3315; Nova Lima: MCNAM 225, MCNAM 469-472; Patrocínio: MCNAM 2683-2685; Santana do Riacho: MCNAM 1946-1964, MCNAM 2739, MCNAM 2770-2772, MCNAM 3494-3495; São Domingos do Prata: MCNAM 1009; São Gonçalo do Rio Abaixo: MNRJ 24881-24897; Belmiro Braga: MNRJ 27554-27555. SÃO PAULO: Ribeirão Branco: MNRJ 18260-18268, MNRJ 18698-18702; Santo André: EI 2890-2894. SANTA CATARINA: Rio Vermelho: EI 2954 (WCAB 6734). RIO GRANDE DO SUL: Santa Maria: MNRJ 18763-18766.

*Physalaemus deimaticus* – BRAZIL: MINAS GERAIS: Santana do Riacho: MNRJ 46859-46860.

*Physalaemus enesefae* – BRAZIL: AMAPÁ: Mantecal: ZUEC 9352.

*Physalaemus ephippifer* – BRAZIL: RORAIMA: Ilha de Maracá: ZUEC 6777. PARÁ: Altamira: ZUEC 7375-7376, ZUEC 7385.

*Physalaemus erikae* – BRAZIL: BAHIA: Guaratinga, Fazenda Vista Bela: MNRJ 30349 (holotype), MNRJ 30343-46 (paratypes); Porto Seguro, Reserva Particular do Patrimônio Natural (RPPN) Estação Vera Cruz: MNRJ 28981-28983 (paratypes), MNRJ 28985 (paratype); Itamaraju, Fazenda Princesa do Pajaú, MNRJ 28984 (paratype); Jussari, Serra do Teimoso: MNRJ 30347-30348 (paratypes), MNRJ 30028-30029 (paratypes), MCN 2198-2199 (paratypes), MCN 2203 (paratypes).

*Physalaemus erythros* – BRAZIL: MINAS GERAIS: Ouro Preto, Parque Estadual do Itacolomi: MNRJ 27986 (holotype); MNRJ 27539 (paratype); MNRJ 30608 (paratype).

*Physalaemus evangelistai* – BRAZIL: MINAS GERAIS: Santana do Riacho: MZUSP 73747 (paratype), MZUSP 73748 (paratype), MZUSP 77645; MZUSP 77646-77649, MZUSP 76570, ZUEC 2316-2317, ZUEC 2880-2882, ZUEC 2884-2885, ZUEC 11265-11266, ZUEC 11167, MCNAM 2788.

*Physalaemus fernandezae* – ARGENTINA: BUENOS AIRES: AMNH 22128-22139, MZUSP 82303;

*Physalaemus fuscomaculatus* – BRAZIL: BAHIA: Caravelas: MNRJ 28443, MNRJ 2839. MATO GROSSO DO SUL: Miranda: MNRJ 24875. MINAS GERAIS: Andrequicé: MNRJ 24727-24734; Bocaiúva: MCNAM 1259; Conselheiro Mata: MCN 3155-3157; Pirapora: MNRJ 24706-24711; Santana do Riacho: MCNAM 2604, MCN 2738, MCN 2740-2750; Várzea da Palma: MNRJ 24712-24726, MNRJ 24735-24736. PARAGUAI: Assunção: MNRJ 12710-12730; Brejo de Ipuã: MNRJ 12696-12709.

*Physalaemus gracilis* – BRAZIL: PARANÁ: Bituruna: MNRJ 3716, MNRJ 14706-14713. SANTA CATARINA: Campo Belo do Sul: EI 2924, EI 2955-2959; Rio dos Cedros: EI 2960-2961. RIO GRANDE DO SUL: Terra de Areia: UFRGS 2015; General Câmara: UFRGS 1914; Torres: MNRJ 31156-31157; Tramandaí: UFRGS 1614-1616; Encruzilhada do Sul: UFRGS 1672; Eldorado do Sul: UFRGS 1833; Porto Alegre: UFRGS 1076; Reserva Ecológica do Taim, Santa Vitória do Palmar: UFRGS 727-728.

*Physalaemus henselii* – BRAZIL: RIO GRANDE DO SUL: Eldorado do Sul: UFRGS 1834, UFRGS 1835; General Câmara: UFRGS 1916, UFRGS 1930; Reserva Ecológica do Taim, Santa Vitória do Palmar: UFRGS 248-251; Viamão: UFRGS 513, MCP 67, MCP 150-160; Cambará do Sul: ZUEC 6242; Porto Alegre: MCP 149, MCP 161, MCP 310; Eldorado do Sul: MCP 2148, MCP 2766-2767.

*Physalaemus jordanensis* – BRAZIL: MINAS GERAIS: Poços de Caldas: CFBH 033-034, ZUEC 4479-4480, ZUEC 6257-6258. SÃO PAULO: Campos do Jordão: MZUSP 73716 (holotype), MZUSP 73717 (alotype), AMNH 78233 (paratype), ZUEC 6940-6942.

*Physalaemus kroyeri* – BRAZIL: BAHIA: Itajibá: ZUEC 2974-2977; Maracás: ZUEC 2980-2982; MZUSP 96472-96547.

*Physalaemus lisei* – BRAZIL: RIO GRANDE DO SUL: São Francisco de Paula: MNRJ 25483-25486, CFBH 079, CFBH 3036, UFRGS 590, UFRGS 655, UFRGS 1229, UFRGS 1302, UFRGS 1433, MCP 304, MCP 1609, MCP 1786-1789, MCP 1852-1853, MCP 2533-2537, MCP 2539-2542, MCP 3192, MCP 3336, MCP 3384-3386, MCP 3394, MCP 3403, MCP 3690, MCP 3730, MCP 4941, MCP 4943; Terra de Areia: UFRGS 2034-2036, UFRGS 2013-2014; Porto Alegre: MCP 138, MCP 3319-3321; Bento Gonçalves: MCP 372; Dom Pedro de Alcântara: MCP 1137, MCP 1470; Canela: MCP 1329, MCP 1486-1488, MCP 1785; Caxias do Sul: MCP 1490; Viamão: MCP 2538, MCP 3383; Gramado: MCP 3275; Torres: MNRJ 31154-31155, MCP 352.

*Physalaemus maculiventris* – BRAZIL: ESPÍRITO SANTO: Santa Teresa: MNRJ 28441. RIO DE JANEIRO: Parati: MNRJ 2749, MNRJ 2763, MNRJ 12440-12459, MNRJ 12467-12470; Teresópolis: MNRJ 12834-12835, MNRJ 24938-24940, MZUSP 67383-67390. SÃO PAULO: Paranapiacaba: MZUSP 13918-13919, MZUSP 13922-13925; Serra de Cubatão: MNRJ 24934-24937. PARANÁ: Guaratuba, Serra de Araraquara: MNRJ 1797, MNRJ 9975-10020.

*Physalaemus maximus* – BRAZIL: MINAS GERAIS: Araponga: MNRJ 18810 (holotype), MNRJ 18811 (paratype), MZUFV 2723 (paratype), MZUFV 3917, MZUFV 3719, MZUFV 3873-3878.

*Physalaemus moreirae* – BRAZIL: SÃO PAULO: Sororocaba, Santos: MNRJ 464 (holotype); Boracéia: MZUSP 59935, MZUSP 25867-25870, MZUSP 37565-37568, ZUEC 9113; Caraguatatuba: MZUSP 77060-77061.

*Physalaemus nanus* – BRAZIL: SANTA CATARINA: Florianópolis: MNRJ 12827-12832, CFBH 3205-3206; Rio Vermelho: EI 2963; Blumenau: EI 2964-2967. RIO GRANDE DO SUL: Cambará do Sul: UFRGS 1836-1840.

*Physalaemus obtectus* – BRAZIL: ESPÍRITO SANTO: Linhares: MZUSP 74259 (holotype); MZUSP 74260 (alotype), MNRJ 4025 (paratype), MNRJ 14206-14207 (paratypes), AMNH 78237-78238 (paratypes), EI 9466-9467 (paratypes), MZUSP 74504-74617, MZUSP 76461.

*Physalaemus olfersii* – BRAZIL: MINAS GERAIS: Barão de Cocais: MCNAM 1741; Caeté: MCNAM 865-867; Nova Era: MCNAM 1114; Peçanha: MCNAM 1132, MCNAM 1134. RIO DE JANEIRO: Teresópolis: MNRJ 2098, MNRJ 12826. SÃO PAULO: Botucatu, Lageado: MNRJ 12765-12768; Botucatu: EI 7841-7844; Iporanga: MNRJ 18467; Ribeirão Branco: MNRJ 19356-19357; Bocaina: MZUSP 82873-82889. PARANÁ: Serra de Araraquara, Guaratuba: MNRJ 1917; MNRJ 10328-10332. SANTA CATARINA: São Bento do Sul: MNRJ 12824-12825.

*Physalaemus riograndensis* – BRAZIL: RIO GRANDE DO SUL: Rio Pardo: MNRJ 2576 (paratype), UFRGS 528-529; 4 km sudeste de Osório: MNRJ 2580-2583 (paratypes); Triunfo: MNRJ 25480-25482, CFBH 3203-3204; Charqueada: UFRGS 1514; Uruguaiana: UFRGS 1780-1781; Capão da Canoa: MCP 1753; Guaíba: MCP 3222, MCP 3327, MCP 3330-3331; Arroio do Sal: MCP3338; Candiota: MCP 3958.

*Physalaemus rupestris* – BRAZIL: MINAS GERAIS: Lima Duarte, Parque Estadual do Ibitipoca: MNRJ 10551 (holotype), MNRJ 10553-1054 (paratypes), MNRJ 24812-24824, MZUFV 4083-4084.

*Physalaemus santafecinus* – ARGENTINA: CORRIENTES: Ituzaingó, Estância Santa Tecla: UFRGS 1943-1947, MZUSP 83258-83259.

*Physalaemus spiniger* – BRAZIL: SÃO PAULO: Iguape: MNRJ 18470-18473; Cananéia, Ilha do Cardoso: MNRJ 18474I, MZUSP 83472; Eldorado: MNRJ 18676; Rio Grande: MZUSP 117247; Estação Ecológica da Juréia: MZUSP 75562. PARANÁ: Guaraqueçaba: MNRJ 18475-18476.

*Physalaemus signifer* – BRAZIL: RIO DE JANEIRO: Engenheiro Paulo de Frontin, Morro Azul: MNRJ 21090, MNRJ 21669; Guapimirim: MNRJ 23409-2310; Ilha da Marambaia: MNRJ 19967; Rio de Janeiro, Morro da Covanca, Jacarepaguá: MNRJ 12837-12842; Palmital: MNRJ 30308; Seropédica,

Floresta Nacional Mário Xavier: EI 2804-2829.

*Physalaemus soaresi* – BRAZIL: RIO DE JANEIRO: Seropédica, Floresta Nacional Mário Xavier: EI 1797 (holotype), EI 1798 (alotype), EI 1943-1945 (paratypes), EI 1784-1796 (paratypes), EI 5517-5529.

*Engystomops coloradorum* – EQUADOR: PICHINCHA: Santo Domingo de los Colorados: AMNH 114829 (paratype), AMNH 89749-89750, AMNH 111556, USNM 285962, USNM 28597, USNM 285798-285799, USNM 285800-285801.

*Engystomops petersi* – EQUADOR: MORONA-SANTIAGO: AMNH 94720-94744. COLÔMBIA: PUTUMAYO: Santa Rosa de Sucumbios: AMNH 116328. PERU: LORETO: Yagua Indian Village: AMNH 96360-96374. BRAZIL: AMAZONAS: Igarapé Belém, Rio Solimões: AMNH 97084-97086, AMNH 97090, AMNH 97099, AMNH 97106-97108, AMNH 97128; AMNH 97136, AMNH 97164, AMNH 97170, AMNH 97175, AMNH 97177, AMNH 97183, AMNH 97195, AMNH 97201, AMNH 97216, AMNH 97223, AMNH 97105, AMNH 97120. RONDÔNIA: Montenegro, Cacaúlândia: MZUSP 80876-80886; MZUSP 113366, MZUSP 113370, MZUSP 113372, MZUSP 113376, MZUSP 113386, MZUSP 113391-113393; MZUSP 113395; MZUSP 113404.

*Engystomops pustulatus* – EQUADOR: EL ORO: AMNH 104968; Los Rios: USNM 284066, USNM 284067; Manabi, Bahia de Caraquez: USNM 284022-284033. PERU: PIURA: USNM 153797.

*Engystomops pustulosus* – MÉXICO: VERA CRUZ: AMNH 63657-63663, AMNH 100515. HONDURAS: AMNH 54935-54936, AMNH 54940-54943; OCOTEPEQUE: Santa Efigênia: USNM 10024-10028. COSTA RICA: GUANACASTE: AMNH 109346-109347; USNM 219785-219789, USNM 219780, USNM 219781. COLÔMBIA: LA GUAJIRA: Piojo: AMNH 75700, AMNH 76184, AMNH 84856-84857, AMNH 88580; USNM 152658-152670. GUATEMALA: ESCUINTLA: AMNH 74396; MNRJ 2784, MNRJ 12484-12489; PANAMÁ: Pearl Island, Isla San José: AMNH 98430-33; COCLÉ: AMNH 98429; CANAL ZONE: AMNH 92662-92666, AMNH 64709, USNM 20356-20357; DARIEN: USNM 140620-140624; CHIRIQUI: Cerro Colorado: USNM 297698-297703; Sapo Montanha, Rio Jesuito: MNRJ 460. TOBAGO: Bacolet R., Is.: AMNH 55866; Buccoo Bay: AMNH 55867; Windward road vic Milestone: USNM 192751; ST. PAUL PARISH: Louis d'or Land Settlement: USNM 192750. TRINIDAD: Maracás: AMNH 92641, AMNH 92647, AMNH 92657, AMNH 55148, AMNH 55819, AMNH 55824, AMNH 51611, AMNH 79841; USNM 166517-166527; Botanic Garden, Port of Spain: USNM

15493-15497, USNM 119054, USNM 15528-15529. VENEZUELA: MNRJ 13083-13085. CARACAS: AMNH 23741, AMNH 70632, AMNH 70637; MONAGAS: Caripito: AMNH 70639-70642.

*Eupemphix nattereri* – BRAZIL: GOIÁS: Luziânia: MCNAM 3000-3006; Silvânia: MNRJ 18245; Nova São Simão: MNRJ 24646-24662; Minaçu MNRJ 24689-24695; MATO GROSSO: Cáceres: MNRJ 24697-246700; Guaicurus: MNRJ 24701-24705. MATO GROSSO DO SUL: Pouso Alto, Águas Claras: MNRJ 31010-31012; Sonora: MNRJ 31013-31015. MINAS GERAIS: Buritis: MCNAM 3277; Manga: MNRJ 24696; Palmital: MCNAM 2886-2887; Patrocínio: MCNAM 2679-2682; Uberlândia: MCNAM 1616-1620, MNRJ 22100-22104; UHE Queimados, Rio Preto: MCNAM 3451; Unai: MCNAM 2869; Varejão de Minas: MCNAM 1984; Várzea da Palma: MNRJ 24636-24645. SÃO PAULO: Lençóis Paulista: MNRJ 24737-24739.

*Pleurodema brachyops* – BRAZIL: RORAIMA: Vila Surumu: MNRJ: 26514-26843.

*Pleurodema diplolistris* – BRAZIL: SERGIPE: Brejo Grande: MNRJ 24920, MNRJ 24923-24932. MINAS GERAIS: Cristália: MNRJ 26164-26166.

*Pseudopaludicola falcipes* – BRAZIL: MINAS GERAIS: Augusto de Lima: MCNAM 521-526, MCNAM 565; Diamantina, Conselheiro Mata: MCNAM 529-531, MCNAM 544-547, MCNAM 551-555; Várzea da Palma: MNRJ 30412-30429; Riacho dos Machados: MCNAM 293-297, MCNAM 609-614. RIO GRANDE DO SUL: Santa Maria: MNRJ 18783-18790; Torres: MNRJ 31158-31174.

*Pseudopaludicola mineira* – BRAZIL: MINAS GERAIS: Santana do Riacho: MCNAM 2437-2451, MNRJ 30621-30639.

#### CLEARED AND STAINED SKELETAL SPECIMENS

*Physalaemus aguirrei* – BRAZIL: ESPÍRITO SANTO: Linhares: MNRJ 22759 (♀), MNRJ 22786 (♂).

*Physalaemus albifrons* – BRAZIL: CEARÁ: Brejo Santo: MNRJ 24063 (♀), MNRJ 24064 (♂).

*Physalaemus albonotatus* – BRAZIL: MNRJ 12756 (♀), MNRJ 12754 (♂).

*Physalaemus barrioi* – BRAZIL: SÃO PAULO: São José do Barreiro: MZUSP 84824 (♂).

*Physalaemus biligonigerus* – BRAZIL: RIO GRANDE DO SUL: Uruguaiana: UFRGS 1776 (♂).

*Physalaemus caete* – BRAZIL: ALAGOAS: Murici: MNRJ 9717 (♂).

*Physalaemus centralis* – BRAZIL: MINAS GERAIS: Várzea da Palma e Pirapora: MNRJ 26505 (♀), MNRJ 26507 (♂).

*Physalaemus cicada* – BRAZIL: BAHIA: Carnaíba: MZUSP 83562 (♀), MZUSP 83570 (♂).

*Physalaemus crombiei* – BRAZIL: ESPÍRITO SANTO: Aracruz: MNRJ 17722 (♀), MNRJ 17740 (♂).

*Physalaemus cuqui* – ARGENTINA: LEDESMA: Yuto: FML 01281-01282 (♀ and ♂).

*Physalaemus cuvieri* – BRAZIL: MINAS GERAIS: Santana do Riacho: MCNAM 3494 (♂), MCNAM 1950 (♂), MCNAM 1957 (♂), MCNAM 3495 (♀).

*Physalaemus fuscomaculatus* – BRAZIL: MINAS GERAIS: Várzea da Palma: MNRJ 24722 (♀), MNRJ 24715 (♂).

*Physalaemus gracilis* – BRAZIL: PARANÁ: Bituruna: MNRJ 14709 (♀). RIO GRANDE DO SUL: Tramandaí: UFRGS 1615 (♂).

*Physalaemus henselii* – BRAZIL: RIO GRANDE DO SUL: Santa Vitória do Palmar: UFRGS 248 (♂).

*Physalaemus kroyeri* – BRAZIL: BAHIA: Maracás: MZUSP 96475 (♀), MZUSP 96531 (♂).

*Physalaemus lisei* – BRAZIL: RIO GRANDE DO SUL: Terra de Areia: UFRGS 2034 (♂).

*Physalaemus maculiventris* – BRAZIL: RIO DE JANEIRO: Parati: MNRJ 12459 (♀), MNRJ 12460 (♂).

*Physalaemus maximus* – BRAZIL: MINAS GERAIS: Araponga: MZUFV 3878 (♂).

*Physalaemus nanus* – BRAZIL: RIO GRANDE DO SUL: Cambará do Sul: UFRGS 1836 (♂).

*Physalaemus obtectus* – BRAZIL: ESPÍRITO SANTO: Linhares: MZUSP 74551 (♀), MZUSP 74601 (♂).

*Physalaemus olfersii* – BRAZIL: SÃO PAULO: Botucatu, Lageado: MNRJ 12765 (♂).

*Physalaemus riograndensis* – BRAZIL: RIO GRANDE DO SUL: Rio Pardo: UFRGS 529 (♂).

*Physalaemus rupestris* – BRAZIL: MINAS GERAIS: Lima Duarte: MNRJ 24824 (♂).

*Physalaemus santafecinus* – ARGENTINA: Ituzaingó: UFRGS 1947 (♂).

*Physalaemus signifer* – BRAZIL: RIO DE JANEIRO: Guapimirim: MNRJ 23410 (♂), MNRJ 23409 (♂).

*Physalaemus spiniger* – BRAZIL: SÃO PAULO: Iguape: MNRJ 18470 (♂).

*Physalaemus soaresi* – BRAZIL: RIO DE JANEIRO: Itaguaí: EI 5517 (♂), EI 5525 (♀).

*Engystomops petersi* – BRASIL: RONDÔNIA: Cacaulândia: MZUSP 113393 (♂).

*Engystomop pustulosus* – MNRJ 12487 (♂).

*Eupemphix nattereri* – BRASIL: MINAS GERAIS: Uberlândia: MNRJ 22104 (♀). GOIÁS: Nova São Simão: MNRJ 24660 (♂).

*Pleurodema brachyops* – BRASIL: RORAIMA: Vila Surumu: MNRJ 26676 (♀), MNRJ 26708 (♂).

*Pleurodema diplolistris* – BRAZIL: SERGIPE: Brejo Grande: MNRJ24931(♀), MNRJ 24929 (♂).

*Pseudopaludicola mineira* – BRASIL: MINAS GERAIS: Santana do Riacho: MCNAM 2451 (♀), MCNAM 2450 (♂).

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